Diving Beetles of the World

Systematics and Biology of the Dytiscidae

Kelly B. Miller and Johannes Bergsten

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Biology of the Dytiscidae

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To Mom and Dad, who made me curious, and to all my students, who keep the adventure alive. — K. B. Miller

To Anders N. Nilsson for being an endless source of inspiration and for contagiously sharing his passion for water beetles, entomology, and systematics. — J. Bergsten

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Preface

Discovering and organizing the diversity of life on Earth (the "natural system") are some of the greatest scientific undertakings of mankind. Students of diving beetles have benefited from some of the best historical systematists who built a strong foundation for our current generation. Study of diving beetle systematics has progressed dramatically in the past several years with great numbers of new species described, many from habitats only newly discovered to have diving beetles. Fortunately, modern phylogenetics using DNA sequence data and sophisticated analytical techniques has made the evolutionary history of diving beetles more accessible, and a natural classification based on their phylogeny is being constantly improved. Organization and improvements to the historical nomenclature have been largely completed. Finally, much has been advanced about the potential utility of diving beetles for studies of biogeography, evolution, community ecology, macroecology, chemical ecology, and sexual strategy evolution. Given all this, it seemed to us a good time to summarize the known world diversity of the group in a book form.

Systematics knowledge is acquired over long periods of time, and changes are to be expected as new taxa and characters are discovered. We expect that this book is not (and should not be) a final word on the study of dytiscid biodiversity. Rather, we hope it will inspire further research and testing of the systematics conclusions presented here. Also, this is a large assemblage of information to gather, and it is likely that there are errors or omissions that we hope can be forgiven. A number of great diving beetle systematists has inspired us, including but not limited to Frank and John Balfour-Browne, Henry Fall, Felix Guignot, John LeConte, Robert Roughley, Maurice Régimbart, David Sharp, Paul Spangler, Frank Young, and Alois Zimmermann. To them and other pioneers we are ever grateful.

This book would also not have been possible without the generous help of many mentors, collaborators, and students over the years who trained us, did the lab work, suffered hardships in the field, laughed with us, talked us out of bad ideas, encouraged us, challenged us, and otherwise formed the scaffolding on which we were able to build this project. Where the book is excellent, they deserve considerable credit. The errors, however, belong to us. We first and foremost thank our graduate academic mentors, Boris Kondratieff, Anders N. Nilsson, and Quentin Wheeler, who inspired us and provided the liberty and resources to explore our taxon. Also, to the following colleagues, we humbly offer our sincere thanks: M. Samuel Adams, Yves Alarie, Robert Angus, Stephen Baca, Michael Balke, Luca Bartolozzi, David Bilton, Olof Biström, Rafael Braga, Gracen Brilmyer, Rasa Bukontaite, Stephen Cameron, Gilbert Challet, Emma Cleary, Lauren Cleavall, Jason Cryan, Aurélie Désamoré, William Edelman, Georgia Evans, Erin Fenton, Hans Fery, Garth Foster, Marco Gaiani, Joja Geijer, Hemant Ghate, J. Randy Gibson, R. Antonio Gomez, Traci Grzymala, Grey Gustafson, Jiri Hajek, Lars Hendrich, Anna Hjalmarsson, Alicia Hodson, Emily Hodson, Sandra Holmgren, Juri and Nicholas Homziak, Heidi Hopkins, Roger Härdling, Toshio Inoda, Benjamin Isambert, Manfred Jäch, April Jean, Sarah Jogi, Luis Joly, Kristina Karlsson Green, Martita Lara, David Larson, Matthew Leister, Richard Leschen, Nathan Lord, Shelley MacNeil, Rachael Mallis, Timothy McCabe, Michael Medrano, Mariano Michat, Elizabeth Montano, Jérôme Morinière, Gino Nearns, Shuhei Nomura, Fernando Pederzani, Philip Perkins, Pyotr Petrov, Felix Picazo, Roberto Poggi, Aaron Prairie, Tolotra Ranarilalatiana, Jacquelin Randriamihaja, Caroline Rempe, Ignacio Ribera, Robert Roughley, Desi Sanchez, Kayla Sayre, Emily Schmeltzer, Amber Schwettmann, Helena Shaverdo, Andrew Short, Robert Sites, Paul Skelley, Jessica Smith, Paul Spangler, Warren Steiner, Gavin Svenson, Nicole Telles, Geoff Thomson, Mario Toledo, Patricia Torres, Emmanuel Toussaint, Julie Urban, Ernie Valdez, Bo Wang, Chris Watts, Hans Weeks, Gunther Wewalka, Michael Whiting, G. William Wolfe, Karen Wright, Donald Yee, and Isabelle Zürcher-Pfander. We also wish to express considerable thanks to our families, who, over the years, provided much needed support and encouragement in so many ways.

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Diving Beetles of the World

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1. Introduction

Diving beetles, or *predaceous* diving beetles, are members of the beetle family Dytiscidae, a name derived from the Latin word for "diver." The actual Latin word is *dyticus*, and, therefore, *dytiscus* may be an incorrect spelling. Nevertheless, that is the spelling of a genus, *Dytiscus*, one of the 188 genera of diving beetles currently recognized and one of the 25 original genera of beetles established by Linneaus (1758) at the beginning of biological nomenclature. At that time the group included most of the beetles that live in the water, and many species then in *Dytiscus* were later classified in other families.

With over 4,300 species known worldwide (Nilsson, 2001; 2003c; 2004; 2008; 2015; 2016; Nilsson and Fery, 2006) and representatives in nearly all types of aquatic habitats, diving beetles have had a long history of study by many great beetle taxonomists. The group has experienced intense efforts to develop a classification that is both comprehensive and natural. The past few years have seen several major advances in diving beetle taxonomy, including a comprehensive world catalog (Nilsson, 2001) and phylogenetic analyses based on morphological (Miller, 2001c), molecular (Ribera *et al.*, 2002b; 2008), and combined (Miller and Bergsten, 2014a) data sets. A recent edited volume also summarized much of the knowledge of the biology and ecology of Dytiscidae (Yee, 2014). However, a single volume presenting a comprehensive treatment of all the genera of diving beetles of the world has not been undertaken since Sharp's (1882) masterpiece, "On aquatic carnivorous Coleoptera or Dytiscidae," over 130 years ago. That monumental work revised the entire taxon then including about 200 genera and 1,140 species, and formed a robust foundation for advancing diving beetle knowledge for many decades. This new volume presents a review of all currently recognized taxa of diving beetles of the world at and above the genus rank. An understanding of their diversity would be incomplete without a review of their natural history and other aspects of their biology, and that is provided below.

Life History and Behavior

Aquatic life.

Diving beetles, in general, are well adapted for an aquatic lifestyle, and adults and all larval stages live in the water. Adults are smooth and streamlined and usually compact in form. Their body shape and size are often somewhat correlated with habitat preferences, with elongate, more narrowed species, such as *Coptotomus* (see Fig. 21.3) often being better swimmers, and short, compact species, such as members of *Pachydrus* (see Fig. 34.4), being more maneuverable and often found in dense vegetation where they do less open-water swimming (Wolfe and Zimmerman, 1984; Ribera *et al.*, 1997). Most have an exceptionally enlarged metacoxa (see Fig. 2.1) for origination of very large muscles inserting on the metatrochanter that drive the metathoracic swimming legs. The tibia, femur and/or tarsi of each leg, but especially the metathoracic legs, are often flattened or laterally expanded and paddle-like and typically have long fringes of natatory setae used for swimming. These setae spread out, and flattened surfaces are turned to provide maximum surface area for pushing against the water during the thrusting leg movements (the power phase) that propel the beetles through the water. Setae collapse against the leg, and legs are turned to minimize the surface area as they are brought back forward before the next thrusting stroke (the recovery phase). Unlike terrestrial beetles, and many water beetles, which alternate leg movements on each side, diving beetle legs move simultaneously when swimming, like oars on a boat.

Although the complex surface sculpturing exhibited by many diving beetles — including striae, impressed microreticulation, punctures, and even setae — might be thought to interfere with hydrodynamics, these features largely exist within the boundary layer of water around the beetle, which travels along with it as it swims (Wolfe and Zimmerman, 1984). Thus they do not interfere with a beetle's ability to swim. Instead, these structures may even serve to help hold the boundary layer or make it thicker while swimming (Wolfe and Zimmerman, 1984).

Diving beetle adults are typically positively bouyant, but they can change their degree of buoyancy somewhat by adjusting the amount of air under the elytra as well as by ingesting water that is stored in an expandable region in the gut (Hicks and Larson, 1991). Larvae (except Dytiscinae) sink in the water.

Most larvae crawl, but some, such as those

of Dytiscinae, live in open water and are strong swimmers, often doing so by "shrimping" movements, or abrupt contractions of the entire body. Many other larvae swim using movements of the legs, which often have well-developed natatory (swimming) setae. Larvae may burrow somewhat, live on the substrate where they creep about, actively swim through the water, or even float, depending on the taxon (Balduf, 1935).

Dytiscids are all, with few rare exceptions, aquatic, but most adults and larvae breathe atmospheric oxygen. To facilitate that, adults carry a bubble of air with them under their elytra where the spiracles (the openings to the tracheal system) are located. They have to occasionally come to the surface to replenish the oxygen in the bubble once it is depleted, and this they do by extending the tip of the abdomen through the surface film. While resting underwater, they also often extend the subelytral bubble out into the water, where it may act as a physical gill with gases exchanging between the bubble and the water column. To escape, adult diving beetles may also expel the air from under the elytra to make themselves less buoyant, and they have to subsequently surface to replenish the air supply. Coming to the surface is potentially dangerous, and diving beetles minimize the need to do it. Many species, particularly of smaller Hydroporinae, or species that live in high-oxygen environments, such as faster streams, may exchange oxygen directly through the cuticle or through specialized pores (Madsen, 2009; 2011). Many larvae must also surface regularly to breathe particularly larger ones or later instars, but early instars (life stages between molts) and small larvae are able to exchange gases through the cuticle. Larvae replenish the oxygen in their tracheae through spiracles at the end of the "siphon," the elongated last abdominal tergum. The first two (of three total) larval instars lack thoracic and abdominal spiracles except the pair at the end of the abdomen. The last (third) larval instar usually has a pair of spiracles on each side of the meso- and metathorax and the abdominal segments. This life stage lives in the water, but also must emerge from the water and find a terrestrial place to pupate, so spiracles and a more open tracheal system may help facilitate the exertion. Larvae of only one group, the genus *Coptotomus*, have gills in the form of elongate lateral extensions on each side of the abdomen.

Dispersal.

Although aquatic, many adult diving beetles are exceptionally vagile and able to fly well to disperse to new habitats. They are especially active at night and often come to lights in large numbers. They occur in very remote habitats such as desert pools and oceanic islands. But, like other highly diverse groups, there is also a diversity of dispersal ability. Species in habitats with high disturbance regimes, such as vernal pools, desert rock pools, phytotelmata, etc., tend to be more prone to frequent dispersal. In tropical areas, members of the genus *Copelatus* often occur in extremely small aquatic habitats such as leaf bracts or tree holes, and during rains they can be found flying throughout the forest seeking newly formed habitats. In some cases, diving beetles may move from more permanent sites to new habitats derived from seasonal rains or melting snow, and then migrate back to more permanent sites when the ephemeral habitats dry (Hilsenhoff, 1986). Species characteristic of more stable habitats, such as streams, are less likely to disperse, in general, and many of these have lost the ability to fly at all. An extreme form of this is the subterranean dytiscid fauna. In these environments with long-term stability, and reduced opportunity to find other suitable sites in which to live, these taxa have largely lost the ability to swim well or fly. Some species may be flightless or dimorphic with respect to flight, and the ability to fly may depend on the season, population size, or other factors (Jackson, 1952; 1955; 1956a; b; Spangler and Gordon, 1973; Bilton, 1994a). In some cases flight may be facultative, and flight muscles may be broken down at a point in the season when the energy derived from them is used for gamete development or other purposes (Bilton, 1994a).

Diving beetles make use of reflected, polarized light, at least in part, to identify potential water bodies during dispersal flights, which explains the reason they are attracted to certain-color cars or other surfaces that similarly reflect polarized light (Schwind, 1995; Nilsson, 1997; Kriska *et al.*, 2006).

In order to disperse, diving beetles must navigate through the water surface film, no small task for small beetles. They typically climb out of the water on emergent structures and often wait a while before taking flight, presumably to dry. The only diving beetle (the only water beetle) known to take flight by moving directly through the surface film and taking flight from the water surface is *Coelambus salinarius* Wallis (Miller, 2013a). Entering the water body through the surface film is not generally a problem for large diving beetles, but smaller ones can have some difficulty and become trapped. These beetles have developed characteristic body movements to help get through the surface film, and may use pygidial gland secretions to increase wettability of the cuticle (Brancucci, 1977; Dettner, 1985).

Cues influencing dispersal have only begun to be investigated, but, for at least some species, factors include the density of conspecifics, plants, and prey as well as water depth, and species vary in the cues to which they respond (Yee *et al.*, 2009). Dispersal biology of dytiscids was recently reviewed by Bilton (2014).

Feeding.

Most diving beetles, as far as is known, are exclusively fluid-feeding predators as larvae. They capture prey and feed with large, sickle-shaped mandibles. The mandibles have a medial channel through which saliva and enzymes are released into the prey item, and fluids from the prey item are sucked into a closed mouth. Exceptions to this are larvae of *Copelatus* and *Hydrotrupes,* which lack the mandibular channel and have shorter, medially serrate mandibles and a better-developed crop, suggesting that these larvae ingest solid food (Ruhnau and Brancucci, 1984; Beutel, 1994). Larvae can be voracious predators feeding on a wide range of prey, including smaller vertebrates (Wilson, 1923; Drummond and Wolfe, 1981; Holomuzki, 1986). Other species generally feed mainly on other insects, like mosquito larvae (James, 1965). Some species appear to specialize, including certain *Dytiscus* with larvae that target case-making Trichoptera (Johansson and Nilsson, 1992). Smaller species, such as Hydroporinae, probably feed mainly on microcrustacea. The mandibular/nasale configuration may optimize capture and feeding on these prey items (Matta, 1983). Prey detection probably includes tactile and chemical cues, but also visual scanning, which may explain the enlarged stemmata and unique retinal configuration present in Eretini and Aciliini larvae (Mandapaka *et al.*, 2006; Buschbeck *et al.*, 2007; Stecher *et al.*, 2010; Stowasser and Buschbeck, 2012). Larvae may engage in ambush predation, active hunting, or combinations of these (Yee, 2010). The amount of vegetation may influence hunting strategy, and high plant density may influence predation among diving beetle larvae, possibly even providing some explanation for diving beetle richness in certain habitats (Yee, 2010).

Adults are carnivorous, feeding on captured prey or recently dead animal material. Although assumed by nearly all historical authors to be entirely animal feeding (thus "predacious" diving beetles), adult beetles are known to feed at least occasionally on plant material (Deding, 1988), but it is not known to what extent this is necessary for their diet. In captivity, diving beetle adults are able to thrive and lay eggs feeding on animal tissues with no plant component (Miller, unpublished). Some of the larger species feed on vertebrate prey (Drummond and Wolfe, 1981; Roy and Sinha, 2002). In some cases, adults have been observed feeding on insects at the water's surface (Smith, 1973; Larson *et al.*, 2000).

No doubt, diving beetles compete for food, certainly with other species (including other predatory insects), probably with other conspecifics, and perhaps between life stages. Multiple adults, though, will regularly feed on the same food item in a "feeding frenzy" (Smith, 1973). Holomuzki (1985a; b) found different microhabitat use by *Dytiscus dauricus* Gebler larvae (diurnal in open water) and adults (nocturnal in vegetation), which might be attributable to competition avoidance. *Cybister chinensis* Motschulsky change their prey preferences between larval instars and adults (Ohba, 2009). Other aspects of competition for resource usage have not been extensively studied, however. Diving beetle predatory habits were recently reviewed by Culler *et al.* (2014).

Defense.

Diving beetle adults and larvae are, at least potentially, preyed upon by vertebrates such as birds and fish, and there are many scattered examples of dytiscids in the foods of these vertebrate predators. In some cases, evidence of attacks by vertebrate predators may be present as scratches in the cuticle (Peddle and Larson, 1999). They are also probably the prey of other vertebrate and invertebrate predators including aquatic mammals (e.g., otters) and insects such as Hemiptera, Odonata, and, perhaps especially, other diving beetles. They have a variety of ways of defending against potential predators. Larger diving beetle adults are able to kick with metathoracic legs bearing large spurs. Both adults and larvae can bite, though only the largest can inflict significant pain, in some cases even breaking the skin of humans and drawing blood. Some specimens, such as larvae of Cybistrinae, exhibit thanatosis, remaining still to avoid detection. The main defensive strategies in both adults and larvae are cryptic coloration and rapid swimming to escape potential predators. Many diving beetles have complex coloration that makes them difficult to see even under the best conditions, but they also are generally most active at night. Many are extremely strong swimmers, and when threatened swim rapidly and erratically. It should not be assumed that all members of the group are strong swimmers, however. Many spend more time crawling over the substrate than actively swimming, but hide quickly when the water is disturbed.

Diving beetles produce a large diversity of defensive chemicals from two main sets of large, exocrine glands. The first are in the prothorax and open at the anterolateral angle of the pronotum. The second pair are in the apex of the abdomen and open on the pygidium. The anterior prothoracic glands are unique to Dytiscidae, though Paelobiidae also have posterior prothoracic glands that may or may not be homologous since they open more anteriorly in dytiscids and are musculated (Forsyth, 1968; 1970; Balke *et al.*, 2005; Beutel and Leschen, 2005; Dettner, 2014). These appear to be the primary defensive glands associated with diving beetles. When a specimen is captured, large volumes of prothoracic gland constituents are often released, and the compounds are known to inhibit feeding by fish (Miller and Mumma, 1976a; b; Gerhart *et al.*, 1991), though not all the compounds do so and may instead be emulsifiers or cannabimimetics (Schaaf and Dettner, 2000). This material often has a very characteristic odor. Chemicals produced and released include a large variety of steroids (Schildknecht *et al.*, 1969; Chadha *et al.*, 1970; Miller and Mumma, 1973; 1974; Chapman *et al.*, 1977; Meinwald *et al.*, 1998; Schaaf *et al.*, 2000; Schaaf and Dettner, 2000) and other compounds (Schaaf and Dettner, 2000). It is thought that gut microorganisms are involved in development of the steroid chemicals produced by the glands (Jungnickel and Dettner, 1997; Schaaf *et al.*, 2000).

Pygidial glands are characteristic of Adephaga (Dettner, 1985). Unlike their Carabidae counterparts, which have relatively simple pygidial gland products, dytiscids have a soup of complexity (Schildknecht, 1970; 1976; Dettner, 1979; 1985; Dettner and Schwinger, 1980). Pygidial gland products include benzoic acid, p-hydroxybenzoic acid methylester, phenylacetic acid (Dettner, 1985), tiglic acid (Dettner and Schwinger, 1980), unsaturated acids (Schildknecht *et al.*, 1983), and 3-indoleacetic acid (a plant auxin; Dettner and Schwinger, 1977), among others. The glands are not strongly musculated in dytiscids, as they are in Carabidae (Dettner, 1985), and they do not generally release products when a diving beetle is handled, unlike the prothoracic glands, suggesting they may not be used defensively against potential predators. Many Adephaga, such as Carabidae and Gyrinidae, do use them defensively against potential predators, but in Dytiscidae they seem to be used mainly for either increasing wettability or as a defense against microorganisms (Schildknecht and Buhner, 1968; Schildnecht, 1971; Dettner, 1985). Constituents are released when the animal is above water, and the hind legs are used to smear material over the body (Maschwitz, 1967). Assar and Younes (1994) investigated the histomorphology of the glands in *Cybister tripunctatus* (Olivier). Dytiscid chemistry was recently comprehensively reviewed by Dettner (2014).

Many diving beetles are dramatically and attractively marked with fasciae, stripes, or maculae on the dorsal surface. Two main explanations have been suggested, both based on the observation that colorful taxa are often those in clear open water with mineral substrates (Young, 1960; Galewski, 1971; Larson, 1996a), whereas dark-colored species are in habitats with dark substrates or dense vegetation (Balke *et al.*, 1997). The first explanation for the bright patterns is that these are visually disruptive and make the animals harder to see by predators. The second explanation is that the coloration is an example of aposematism for advertising the general distastefulness of the beetles. It is difficult to generalize about either of these since there are many diving beetles in turbid water or dense vegetation that are therefore difficult to see, but nonetheless have dramatic coloration. As well, many diving beetles with chemical defense do not appear to have any warning coloration. Probably it is a combination of several strategies that lead to diving beetle color patterns.

Associations with other organisms.

A number of mite species are known from diving beetles with especially the biology of *Eylais* Latreille species on dytiscids investigated by Aiken (1985). Diving beetles are also attacked by a diversity of Laboulbeniomycetes (Ascomycota) (Majewski, 1988; Majewski and Sugiyama, 1989; Lee and Choi, 1992; Lee *et al.*, 1995; Lee and Lim, 1998; Santamaria, 2001; Rossi and Bergonzo, 2008), many of which are position specific and transmitted during sexual contact (Goldmann and Weir, 2012). Diving beetles have a rich variety of microfauna in the gut (Schaaf and Dettner, 1997), some of which may be implicated in production of prothoracic gland steroid constituents (Schaaf and Dettner, 1998). *Rickettsia* da Rocha-Lima have been isolated from species of *Deronectes* and appear to be vertically transmitted between generations (Kuechler *et al.*, 2009). Microsporidia have been isolated from the gut of *Eretes sticticus* (Linnaeus) (Kalavati and Narasimhamurti, 1976), and gregarines from the gut of a *Dytiscus* species (Baudoin, 1968; Kalavati and Prasada Rao, 1995). A ciliate parasite was described from the esophagus of several Dytiscidae species by Stammer (1948). Jackson (1959) found slime bacteria (Myxobacteria) on dytiscid eggs, though it is entirely unclear what they might be doing there.

Chalcidoid parasitoid wasps in the families Mymaridae and Eulophidae attack diving beetle eggs under water (Jackson, 1958a–c; Zerova and Fursov, 1995), an anthomyiid fly is known to attack diving beetles (Chilcott and James, 1966), and diving beetle pupae are attacked by parasitoid larvae of the Carabidae genus *Brachinus* Weber, as well (Juliano, 1985; Saska and Honek, 2004).

Other aspects of diving beetle ecology.

Diving beetles form consistent, distinctive communities associated with particular habitats, and this has been demonstrated analytically in several regions (Larson, 1985; 1997a; Ranta, 1985; Cuppen, 1986; Eyre *et al.*, 1986; Lancaster and Scudder, 1987; Foster and Bilton, 2014; Lillie, 1991; Nilsson *et al.*, 1994). Many of the species involved in the communities have somewhat different habitat and geographic ranges suggesting varying, but overlapping, environmental tolerances (Larson, 1985). These communities also often have a range of species of different sizes, but often also multiple species of a similar size may be found. Co-occurrence of diving beetles with similar size and habits is common, but is not easily explained, and has not been well investigated (but see Scheffer *et al*., 2015). It is not clear how these species might be competing for similar prey items or other resources (Juliano and Lawton, 1990b). In some cases, species have the same feeding preferences and dispersal tendencies, but occupy slightly different microhabitats (Pitcher and Yee, 2014). Although some sites may have only a few species of diving beetles, great numbers of species have been known to co-occur at the same site with up to or over 50 known, for example, from a boreal pond-marsh habitat in Alberta (Larson *et al.*, 2000), a group of glacial kettle holes in boreal north Sweden (Nilsson, 1982d), at Marais de la Perge wetland, southeastern France (Bameul, 1994), and about as many from small pond habitats in India and Ghana (Miller, unpublished).

Factors affecting diving beetle distributions may include degree of permanence, water movement, size, salinity or other chemical attributes, temperature, seasonal variability, successional stage, exposure, substrate type, plant communities (or absence of plants), and presence of other animals, including potential prey and predators. The degree to which these factors affect diving beetles is only poorly known and only beginning to be investigated. Presence or absence of other competing aquatic predators including Hemiptera, Odonata, and fish probably has a large effect on diving beetle communities (Larson, 1990a). Dytiscidae community patterns were reviewed by Vamosi and Wohlfahrt (2014).

Mating and mating systems.

Dytiscids are highly variable in several attributes of mating systems, including male genitalia, secondary male and female sexual features, internal female genitalic morphology, sperm morphology, and behavior (Miller and Bergsten, 2014b). See under the Morphology section below for a description of male and female genitalia and variation.

Dytiscid sperm exhibits some of the greatest complexity and diversity of any animals (Auerbach, 1893; Ballowitz, 1905; Jamieson *et al.*, 1999; Pitnick *et al.*, 2009; Higginson *et al.*, 2012a; b). Particularly notable are the sperm conjugates characterizing most diving beetles where two or more sperm are attached together (Higginson and Pitnick, 2011; Higginson *et al.*, 2012a; b). These may be simple conjugates of two sperm attached at the head found in many major groups (Mackie and Walker, 1974; Werner, 1976a, b; Jamieson *et al.*, 1999) to complex conjugates of numerous sperm, all attached at the head such as found in a number of groups, especially in Hydroporinae but also in *Agabetes*, *Batrachomatus*, and some Agabinae and Colymbetinae (Ballowitz, 1905; Mackie and Walker, 1974; Werner, 1976a; Dallai and Afzelius, 1988; Higginson *et al.*, 2012a; b). Most dramatic are the "rouleaux" types of conjugates (Fawcett and Hollenberg, 1963; Shepherd and Martan, 1979; Heath *et al.*, 1987), which may include many thousands of sperm all attached together in a chain with the sperm heads nested together. This is found especially in many groups of Hydroporinae (Higginson *et al.*, 2012a; b). Diving beetles also often exhibit sperm heteromorphism with different-sized or -shaped sperm in the same male ejaculate (Voïnov, 1902; Higginson *et al.*, 2012a; b), with some of these, as in *Cybister tripunctatus,* both eupyrene and apyrene (Mukherjee *et al.*, 1989).

Diving beetles exhibit a range of mating behaviors, though there has been little published about this aspect of their natural history, with only one species, *Dytiscus alaskanus* J. Balfour-Browne, studied in any great detail (Aiken, 1992), though others have been referenced more anecdotally (Miller, 2003). Most species appear to have scramble types of mate finding, though presence of stridulatory devices on males in several groups (Larson and Pritchard, 1974) implies sexual signaling by males. Recently, an example of chemical signaling by females of *Rhantus* was first reported (Herbst *et al.*, 2011).

In at least some cases, males and females exhibit intense sexual antagonism (Aiken, 1992; Miller, 2003; Bergsten and Miller, 2007). Diving beetle males are potentially able to hold females underwater during mating, thereby restricting access to air, which may be a coercive male strategy (Miller and Bergsten, 2014b). Females behaviorally resist male coercive efforts (Aiken, 1992; Miller, 2003; Miller and Bergsten, 2014b). This appears to be most evident in Cybistrinae and Dytiscinae where males also have large, expanded, grasping protarsi with (in Dytiscinae) large sucker-shaped adhesive setae ventrally (see Fig. 2.11g), which are used to adhere to resisting females (Aiken, 1992; Bergsten *et al.*, 2001; Miller, 2003). Females of several groups have the dorsal cuticle conspicuously modified with grooves (*Dytiscus*, see Fig. 16.6b,d), grooves and setae (*Acilius*, see Fig. 20.11b), rugosity (*Graphoderus*, *Hyderodes*, *Hydaticus*, Figs. 16.7c,17.2,20.13c), or striae (*Cybister*, *Megadytes*, *Thermonectus*, see Fig. 20.10) that apparently interfere with the sucker devices on males (Bergsten *et al.*, 2001; Miller, 2003; Karlsson Green *et al.*, 2013). This arms race is particularly interesting and unique in Cybistrinae and Dytiscinae since they also have, secondarily derived, some of the simplest female reproductive tract (see Fig. 2.14q) and sperm morphology (Miller and Bergsten, 2014b). In the few species examined for mating, there are a number of stereotyped associated behaviors in addition to female resistance and male persistence, including shaking and male leg-fluttering (Aiken, 1992; Cleavall, 2009). This seems to imply that much of the sexual selection may be occurring in this group prior to insemination (Miller and Bergsten, 2014b). The opposite is true of Hydroporinae, which have incredibly complex and diverse female RT morphology and sperm conjugation, but seemingly simple behaviors (Miller, 2003; Cleavall, 2009; Miller and Bergsten, 2014b). This suggests that much of the sexual selection in the group is occurring after insemination during cryptic female choice and sperm competition (Miller and Bergsten, 2014b). Miller and Bergsten (2014b) presented a review of dytiscid sexual systems.

Development.

Eggs are laid underwater or in the splash zone near water. In some cases they are glued to aquatic plants or other objects; in other cases they are dropped randomly or placed in the substrate. Females with this strategy, such as in *Rhantus*, often have ovipositors that are short and bear numerous tactile setae (Miller, 2001c). In other cases, such as members of Aciliini, the ovipositor is very long and eggs are deposited more deeply in crevices or other hidden places (Miller, 2001c). Finally, several groups of diving beetles have ovipositors that are knife- or saw-like, in which cases the ovipositor is used to cut or slice plant tissue, into which eggs are then inserted (Jackson, 1960b; Inoda, 2011b). Unsurprisingly, given the extreme range of variation in oviposition technique, female ovipositor shape and structure are quite variable across the family (Burmeister, 1976; Miller, 2003). The time between oviposition and hatching depends on the species and things such as water temperature (Aiken, 1986b), time of year, etc. Some species overwinter in the egg stage (Nilsson, 1986c). Often, though, eggs hatch within 5–14 days (Sueselbeck, 2002b).

Dytiscids have three larval instars, and all those known are fully aquatic until they leave the water to pupate. Larval development depends to a certain extent on temperature (Inoda, 2003), but other proximate factors affecting larval development are not well known. Most weight and size gain occurs in instar III (Kingsley, 1985). Instar III larvae have functional spiracles on abdominal segments I–VII which they use when they leave the water to pupate in secluded areas of soil or moss.

Diving beetle pupae and pupation are not well studied. Main (1934) and Holomuzki (1988) investigated pupae, pupation sites, and mortality in *Dytiscus* species. Pupation takes place in a cell that may be near the water or many meters away. Pupae often develop under or next to a structure such as a stone, board, or other obstacle. The cell is constructed by larval movements in the soil, and, in at least some cases, the larval mandibles are used for construction of a chamber (Matheson, 1914). Members of the carabid genus *Brachinus* are known parasitoids of Dytiscidae pupae (Juliano, 1984).

Most studied species (mainly temperate North American and European species) are univoltine or semivoltine. Nilsson (1986c) developed a system for understanding and classifyinig European diving beetle life cycles. He identified five main types of life cycles in these beetles that vary based on whether species are univoltine or semivoltine and the way in which they diapause over the winter. Some species pass the winter as adults, others as eggs, and still others as larvae. Semivoltine species may pass the first winter as eggs or larvae and the second as adults. These types of life cycles are reflected in egg and larval development, with eggs of some species hatching nearly immediately or, in others, nearly a year after oviposition (Nilsson, 1986c). Larvae may similarly have an extended or rapid development, and onset of reproductive maturity of

adults or reproductive diapause varies depending on the life cycle strategies (Nilsson, 1986c). Life cycle strategy and egg, larval, pupal, and adult phenologies vary also with seasonal propensity for migration and climate (Galewski, 1963b; 1966; Nilsson, 1986c; Carr and Nilsson, 1988). There are records of dytiscids moderately active under the winter ice, often discovered by ice fisherman (Roughley, 1990).

Life cycle strategies in tropical species or species with different types of seasonality (e.g., wet versus dry seasons) have been studied considerably less, and certainly not comprehensively. It is likely that dytiscids in these areas may be multivoltine or may receive life history cues from onset of rains or other cycles. Diving beetles in seasonally dry areas may enter a terrestrial diapause, either as egg or adult, until aquatic habitat becomes available again (Garcia *et al.*, 1990). As these habitats dry, they may either remain nearby (Garcia *et al.*, 1990) or be forced to leave the site and seek other habitat. In this case, more permanent reservoirs of water may serve as critical temporary habitats for diving beetles until rains or vernal melting snow provides greater numbers of bodies of water. Sometimes mass migration from a drying habitat happens synchronously, as in *Eretes* species (Kingsley, 1985). In tropical regions, on days with extensive rain, large numbers of diving beetles may arrive at lights (Miller, unpublished), presumably as they disperse to take advantage of potential new habitat. In general, it is clear that tropical diving beetles exhibit greater seasonality than might be ordinarily expected. For example, larvae are much more commonly found during certain times of the year than others (Miller, unpublished).

Chromosomal data have been reported extensively across diving beetles (Smith, 1953; Smith and Virkki, 1976; Saleh Ahmed *et al.*, 1997; 2000; Dutton and Angus, 2007; Angus, 2008; 2010a; b; Angus and Tatton, 2011; Tatton and Angus, 2011; Angus *et al.*, 2013). Sex determination is somewhat variable, with many species XO/XX and others XY/XX, a neo-XY type of sex determination. Total karyotype number is also quite variable, often between relatively closely related species.

Habitats

Diving beetles are found in nearly all types of inland aquatic habitats from lakes and streams to wet surfaces of rocks. Although there are a few terrestrial species, these are rare. Unlike their distant cousins, Hydrophilidae, there are no extensive radiations of terrestrial taxa, and nearly all species of Dytiscidae are in some way closely associated with water. A large number of species appear to be eurytopic, occurring in many habitat types, and these are among the most commonly encountered species in the family. Others are much more stenotopic, occurring only in certain specialized habitats. Any particular species of diving beetles, at any given time, occurs somewhere on a continuum between generalization and extreme specialization in habitat requirements, and it can be difficult to characterize whole groups. Major features influencing diving beetle macro- or microdistributional patterns may be (1) abiotic, such as temperature, size of water body, habitat stability, degree of exposure, substrate type, amount of water movement, or water chemistry, or (2) biotic, includ-

Fig. 1.1. Prairie pond, Converse County, Wyoming, USA. *Agabus disintegratus, Coelambus impressopunctatus, C. sellatus, C. unguicularis, C. patruelis, Dytiscus cordieri, Hydroporus pervicinus, Hygrotus acaroides, H. sayi, Laccophilus maculosus, Liodessus obscurellus, Rhantus binotatus.*

Fig. 1.2. Meadow pond, Nuoru Prov, Sardinia, Italy. *Agabus bipustulatus, A. brunneus, Bidessus goudotii, Colymbetes fuscus, Cybister lateralimarginalis, Dytiscus pisanus, Hydaticus leander, Hydroglyphus geminus, Laccophilus minutus.*

Fig. 1.3. Alpine pool, 4,600m elevation, Peruvian Andes. *Rhantus blancasi*.

Fig. 1.4. Llanos marsh, Apure, Venezuela. *Anodocheilus virginiae*, *Bidessodes evanidus*, *Bidessonotus obtusatus*, *Copelatus* sp., *Derovatellus lentus*, *Desmopachria* sp., *Hydrovatus caraibus*, *Liodessus* sp., *Megadytes carcharias*, *Neobidessus alternatus*, *N. bordoni*, *Vatellus grandis*. Photo by Andrew E.Z. Short. Used with permission.

Fig. 1.5. Desert oasis spring, Skeleton Coast, Namibia. *Cybister gschwendtneri, Herophydrus inquinatus*, *Hydaticus bivittatus*, *Laccophilus lineatus, Philodytes umbrinus.*

ing amount and type of plant material and presence of certain other animals, either prey, potential predators, or competitors for prey. Adults and larvae typi-

Fig. 1.6. Boreal bog with floating mats of *Sphagnum* and *Carex*. Lomtjärn, Umeå, Sweden. *Acilius sulcatus, A. canaliculatus, Agabus bipustulatus, Colymbetes paykulli, C. striatus, Dytiscus circumcinctus, D. lapponicus, D. marginalis, Graphoderus zonatus verrucifer, Hydaticus aruspex, Hyphydrus ovatus, Ilybius similis, I. ater, Rhantus exsoletus, R. suturellus.*

Fig. 1.7. Roadside pool, Ghana. *Bidessus toumodiensis, Cybister burgeoni, C. marginicollis, C. vulneratus, Clypeodytes proditus, Hydaticus dorsiger, H. humeralis, H. lativittis, H. matruelis, H. speciosus, H. ugandaensis, Leiodytes heiroglyphicus, Platydytes coarctaticollis, Uvarus baoulicus, Yola mocquerysi, Y. nigrosignata.*

cally occur in the same habitats, though adults are able to disperse and may be found in a wider range of situations than larvae. Various aspects of dytiscid habitats were recently reviewed by Gioria (2014). Some of the characteristic habitat types containing diving beetles are described below.

Ponds, marshes, bogs, and fens. (Figs. 1.1–11)

By far the most commonly encountered diving beetles are found in lentic (standing water) habitats, typically those with considerable vegetation. Often these habitats may include a huge diversity of dytiscids with, in extreme cases, as many as 40–50 species occurring together, though they may segregate themselves by microhabitat within a larger lentic water body. Some species, such as many

Fig. 1.8. Salt pan, Natrona Co., Wyoming, USA. *Coelambus salinarius.*

Fig. 1.11. Leaf-choked rock hole in limestone karst formation, Ankarana National Park, Madagascar. *Madaglymbus* sp.

Fig. 1.9. Leaf-choked forest pool, Venezuela, *Celina* sp., *Desmopachria* sp., *Hydaticus subfasciatus, Platynectes* sp., *Vatellus tarsatus.* Photo by Andrew E.Z. Short. Used with permission.

Fig. 1.12. Leaf bract phytotelmata, Tambopata, Peru. *Copelatus* sp., *Desmopachria* sp., *Laccophilus* sp., *Thermonectus circumscriptus.*

Fig. 1.10. Forest swamp, Tambopata, Peru. *Agaporomorphus knischi, Anodocheilus maculatus, Bidessonotus obtusatus, Celina sp., Copelatus sp., Derovatellus lentus, Desmopachria sp., Laccophilus adspersus, Neobidessus bolivari, Rhantus calidus, Thermonectus circumscriptus, T. leprieuri, T. variegatus, T. succinctus, Vatellus bifenestratus, V. grandis.*

Bidessini, are found in the extreme margins of such places, or even in margins with wet substrate and no standing water at all, whereas others, such as larger members of Dytiscinae or *Coptotomus,* may be more typically found in deeper reaches. Others, such as *Hydrovatus* or *Celina*, prefer dense vegetation and still others, such as *Thermonectus*, may be in more sparse vegetation or only on mineral substrates.

Some groups specialize in northern bogs and fens or other acidic environments (Fig. 1.6), such as many *Agabus*, *Neoscutopterus,* and certain *Hydroporus*. In some cases, these taxa appear to be nearly terrestrial, living in dense vegetation mats in such bog habitats. Others are extreme halophiles (Fig. 1.8), especially *Coelambus* and *Nebrioporus*. For example, *C. salinarius* Wallis specimens can withstand an exceptional range of salt concentrations, from 12 to 71gL^{-1} (Timms and Hammer, 1988; see also Sánchez-Fernández *et al*., 2010, Céspedes *et al*., 2013, Pallarés *et al*., 2015).

Rivers, streams, and springs. (Figs. 1.13–23)

Although generally not as diverse as lentic faunas, lotic specialists, or rheophiles, are well

Fig. 1.13. Pools in dried-out river east of Maintirano, Madagascar. *Africophilus nesiotes, Bidessus longistriga, B. perexiguus, Copelatus befasicus, C. vigintistriatus, Liodessus luteopictus, Madaglymbus alutaceus, M. fairmairei, M. elongatus, Pachynectes hygrotoides, Philaccolus sp., Uvarus rivulorum, Yola costipennis.*

Fig. 1.14. Rock pools, streambed, White Mountains, Queensland, Australia. *Clypeodytes migrator, Cybister tripunctatus, Hydaticus quadrivittatus, Hydroglyphus trifasciatus, Hydrovatus niger, H. rufoniger, Hyphydrus decemmaculatus, Laccophilus clarki, L. transversalis, Neobidessodes thoracicus.*

Fig. 1.15. Pond in dried river bed in deciduous forest, Kirindy forest reserve, Madagascar. *Cybister cinctus, C. tibialis, C. owas, C. senegalensis, C. vulneratus, Hydaticus petitii, H. sobrinus, H. dorsiger, H. servillianus, Eretes griseus, Rhantaticus congestus*, *Bidessus longistriga, B. perexiguus, Clypeodytes* sp.*, Madaglymbus alutaceus, Pachynectes costulifer, Uvarus rivulorum, Yola costipennis.*

Fig. 1.16. Drying pools in prairie wash, Wyoming, USA. *Agabus griseipennis, Boreonectes striatellus, Coelambus diversipes, C. patruelis, C. sellatus, C. tumidiventris, Copelatus chevrolati, Hygrotus sayi, Laccophilus maculosus, Liodessus obscurellus, Rhantus binotatus, R. sericans.*

Fig. 1.17. Pools in streambed, Flumendosa River, Sardinia, Italy. *Bidessus minutissimus, Deronectes moestus, Meladema coriacea, Nebrioporus clarkii, Stictonectes rufulus.*

represented throughout the Dytiscidae with many larger species diversifications. Diving beetles with lotic preferences are found in most major groups, with some larger groups entirely, or nearly entirely, lotic, like the hydroporines *Oreodytes*, *Heterosternuta*, *Deronectes*, *Hovahydrus*, and *Barretthydrus*. Some species are typical of larger rivers (Fig. 1.22), such as *Batrachomatus* and many *Oreodytes*. Others are more typical of small streams (Fig. 1.18) such as certain *Heterosternuta*, *Rhithrodytes,* or *Austrodytes*. Finally, other groups are characteristic of small seeps or springs (Fig. 1.23), including *Sanfilippodytes*, *Hydrocolus,* and many *Platynectes*.

Some species in these habitats live among interstices along the margins (the hyporheic zone). including members of *Hydrotrupes*, *Glareadessus*, *Carabhydrus*, and others. These species often have a distinctive morphology, elongate, flattened, and with the lateral margins of the body distinctly discontinuous between the pronotum and elytron (e.g.,

Fig. 1.18. Tropical forest stream with leaf pack, Rio Sipapo tributary, Amazonas, Venezuela. *Agaporomorphus sharynae, Hydrodessus* sp., *Desmopachria* sp., *Bidessonotus* sp. Photo by Andrew E.Z. Short. Used with permission.

Fig. 1.19. Great Dividing Range stream, New South Wales, Australia. *Australphilus saltus*, *Batrachomatus daemeli, Barretthydrus tibialis, Carabhydrus niger, Necterosoma susanna, Sternopriscus hansardii*.

Fig. 1.20. Post-monsoonal stream, Mulshi, India. *Hydaticus luczonicus, Microdytes sabitae.*

Fig. 37.61), which may help them with movement in the substrate (Larson, 1991a). Their body form (and lifestyle) is somewhat similar to subterranean species (see below), and some groups, such as *Carab-*

Fig. 1.21. Andean stream, Pisac, Peru. *Lancetes nigriceps.*

Fig. 1.22. Boreal river Öreälv, Ångermanland, Sweden. *Deronectes latus, Nebrioporus depressus, Oreodytes sanmarkii, Platambus maculatus*.

hydrus and *Limbodessus*, have representatives overlapping these habitats.

A number of taxa, like *Melademа, Madaglymbus,* and some *Deronectes*, specialize in pools and micropools along streams, pools in drying streams, and similar situations (Figs. 1.13–17).

Phytotelmata. (Fig. 1.12)

There are often very large numbers of specimens, though lower diversity, in phytotelmata (where water collects in tree holes, palm bracts, bromeliads or other plant-based containers), especially in tropical forests. Some groups, such as many *Copelatus* and *Aglymbus* as well as certain *Laccophilus* and *Desmopachria*, specialize in exploiting these often abundant, but easily disturbed, habitats (Balke *et al.*, 2008; Campos and Fernandez, 2011). These communities generally broadly overlap those in leaf-choked forest pools, though the latter may have their own typical fauna, including, for example, *Hoperius*, *Agabetes,* and *Platynectes*. Given the ephemeral nature of some of these habitats, individuals are,

Fig. 1.23. Rocky spring, Amboli, India. *Lacconectus andrewesi*.

Fig. 1.24. Waterfall margin, hygropetric habitat, Tully Gorge National Park, Queensland, Australia. *Petrodessus conatus*.

Fig. 1.25. Waterfall with hygropetric rockwall habitat, Montagne d'Ambre National Park, Madagascar. *Africophilus* sp.

unsurprisingly, among the diving beetles that fly most readily. They are often found at lights, particularly during or after rains, presumably intercepted as they disperse to seek new habitat. When collected, they often fly immediately from the net.

Fig. 1.26. Inselberg, Venezuela, *Fontidessus toboganensis*. Photo by Andrew E.Z. Short. Used with permission.

Fig. 1.27. Beachside seeps, Seal Rock, Oregon, USA. *Hydrotrupes palpalis*.

Hygropetric habitats. (Figs. 1.24–27)

Hygropetric habitats, where thin films of water flow over rock, are found worldwide but have been undercollected for insects in general. Habitats may be nearly horizontal (Figs. 1.26,27) to nearly vertical (Figs. 1.24,25) with different species through this range. These habitats are becoming increasingly important for knowledge of diving beetle diversity. Venezuela, for example, which has a large representation of this habitat, is yielding an impressive number of hygropetric specialists including *Fontidessus* Miller and Spangler, *Spanglerodessus* Miller and García, and *Incomptodessus* Miller and García (Miller and Spangler, 2008; Miller and Garcia, 2011). It has also produced other higher level Hydradephaga, including the Noteridae tribe Tonerini Miller (2009), and the families Meruidae Spangler and Steiner (2005) and Aspidytidae Ribera *et al.* (2002). This diversity is tantalizingly sugges-

Fig. 1.28. Spring emerging from karst aquifer, head of Caroline Springs, Terrell Co., Texas, USA. *Ereboporus naturaconservatus*.

tive that other regions with extensive hygropetric habitats, such as Madagascar, Australia and Africa, might be similarly productive, and hygropetric diving beetle taxa such as *Africophilus* and *Petrodessus* and many others have been described in different parts of the world (Omer-Cooper, 1957; 1969; Holmen, 1984; Sanfilippo and Franciscolo, 1988; Franciscolo, 1994; Miller, 2012). These taxa often "swim" around on the rock surfaces in small cracks, often on fully exposed, hot surfaces.

Subterranean water. (Figs. 1.28,42)

The first thoroughly hypogean (subterranean) diving beetle was described over 100 years ago (Abeille de Perrin, 1904). Numerous additional taxa were subsequently described from several biogeographic regions (Peschet, 1932; Uéno, 1957; Sanfilippo, 1958; Ordish, 1976b; 1991; Young and Longley, 1976; Larson and Labonte, 1994; Spangler and Barr, 1995; Spangler, 1996; Uéno, 1996; Castro and Delgado, 2001; Wewalka *et al.*, 2007), but these taxa were regarded as rare and unusual anomolies compared with more typical epigean faunas (Young and Longley, 1976). During the past decade, however, the discovery of an exceptionally diverse subterranean fauna in Western Australia has resulted in a modification of this view with nearly 100 species described from paleodrainages (Watts *et al.*, 2007; Leys and Watts, 2008). Species recently discovered from southeastern Asia (Spangler, 1996), Europe (Ribera and Faille, 2010) and southern United States (Miller *et al.*, 2009b; Jean *et al.*, 2012) also suggest that this fauna may be considerably more rich than known, but the obvious difficulty in collecting this habitat has made discoveries problematic. Only a few species have been found in caves, with most found in wells, boreholes, or washed out of springs.

Subterranean diving beetles (see Fig. 3.51) are characterized by depigmentation, reduction of the compound eyes, loss of flight (often entire loss of wings and fusion of the elytra), and development of a characteristic shape with distinct discontinuity in the lateral curvature between the pronotum and elytra and shortening of the prosternal process. Reduction of many features that are typically used to group diving beetles combined with much convergence in features related to the subterranean syndrome have made discovering relationships of subterranean taxa with epigean dytiscids problematic. Use of molecular data has made understanding the relationships of the Australian subterranean fauna possible, and these have been investigated in greater detail than others in the world (e.g., Leys and Watts, 2008). The North American species belong to at least three Hydroporinae lineages (Miller *et al.*, 2013). The bulk of diversity in this habitat type belongs to Hydroporinae, especially Bidessini and Hydroporini, though Hyphydrini (Wewalka *et al.*, 2007) also has representatives, and there are a few examples of subterranean Copelatinae (Balke *et al.*, 2004c; Watts and Humphreys, 2009). The larvae that are known are also subterranean (Alarie *et al.*, 2013), but no pupae have been characterized. Since diving beetle pupa are terrestrial, it will be interesting to discover the pupation sites of groundwater species.

Terrestrial habitats.

Many diving beetle taxa live in situations that are, in many respects, nearly terrestrial, including muddy margins of bogs, streams and ponds, seeps, or hygropetric habitats. Many species overwinter or outlast temporary dry seasons in terrestrial circumstances. And certainly most diving beetles can enter the terrestrial environment to disperse and live out of the water for quite some time. As far as is known, however, all species require water for completing their life cycles. Only five species of diving beetles that are putatively terrestrial as their exclusive adult habitat have been described, including two *Geodessus* Brancucci (Bidessini) from India and Nepal (Brancucci, 1979; Balke and Hendrich, 1996), one species in *Typhlodessus* (Bidessini) from New Caledonia (Brancucci, 1985b; Brancucci and Hendrich, 2010), and two *Paroster* (Hydroporinae, Sternopriscina) species from northern Australia (previously in *Terradessus*; Watts, 1982; Brancucci and Monteith, 1996). These have been collected by sifting leaf litter, so it has been difficult to establish for certain whether they are exclusively terrestrial. They lack many features of more typical swimming beetles, including natatory (swimming) setae on the

legs, and field experiments with *Geodessus* clearly indicate they are unable to swim (Brancucci, 1985a). Larvae are unknown for these taxa, and it is not clear whether they, too, are terrestrial.

Fossil History

Permian-Triassic (299–201 mya). (Fig. 1.29)

According to some recent fossil discoveries, the evolutionary history of Adephagan water beetles starts in the Permian period (299–252 mya). The extinct aquatic family Triaplidae is known from the Mal'tsevo formation at Babii Kamen, Russia, which is dated to late Permian or early Triassic (Volkov, 2013). Gosh *et al.* (2007) described a potential but very doubtful dytiscoid larvae from the Parsora formation, India, also of late Permian or early Triassic origin. A fossil larva of Permian age, *Permosialis*, has been suggested to be a Gyrinid larvae, but this is contested and refuted by most today (Beutel *et al.,* 2013; Prokin *et al.,* 2013). Although yet unpublished, Prokin *et al.* (2013) mention a dytiscoid fossil from layers in the Yinping Formation, China, which are dated to middle Permian (Lin *et al.,* 2010). This would be the oldest known fossil of the superfamily Dytiscoidea known to date. Dytiscoidea includes the extant families Dytiscidae, Paelobiidae, Amphizoidae, Aspidytidae, Meruidae, and Noteridae as well as the extinct families Liadytidae, Parahygrobiidae, Coptoclavidae (excluding Trimarchopsinae *sensu* Beutel *et al.,* 2013), and possibly Colymbotethidae (Ponomarenko, 1993).

Jurassic (201–145 mya). (Fig. 1.29)

The oldest fossil currently placed in the family Dytiscidae is *Palaeodytes gutta* Ponomarenko from late Jurassic deposits at Karatau, Kazakhstan (Ponomarenko, 1987). Other species of *Palaeodytes* have also been described from early Cretaceous deposits from Russia and from the United Kingdom (Ponomarenko *et al.,* 2005). An early Jurassic well-preserved fossil larvae, *Angaragabus jurrassicus* Ponomarenko, morphologically similar to Agabinae larvae, is now considered to be closer to Aspidytidae or Liadytidae (Prokin *et al.*, 2013). Likewise the Jurassic *Hydroporus petrefactus* Weyenbergh from Bavaria, Germany, is doubtfully a diving beetle, let alone a *Hydroporus* (Prokin and Ren, 2010). Diving beetles, according to the fossil record, therefore originated in the Jurassic but were not common, and other Adephagan water beetles, especially Coptoclavidae, dominated during this time. (Beutel *et al.,* 2013).

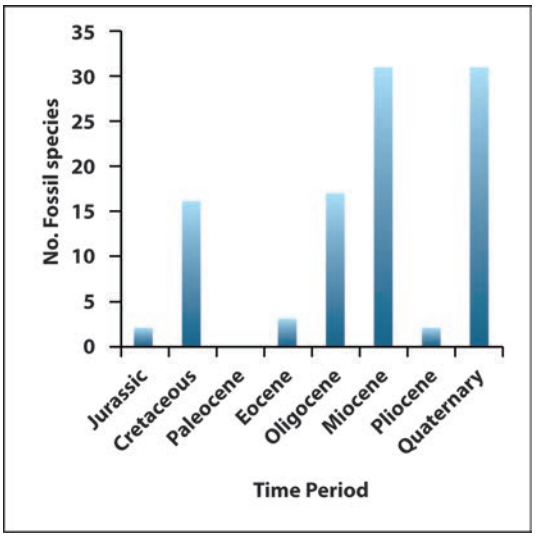


Fig. 1.29. Number of fossil species of Dytiscidae described from each time period after Nilsson (2015).

Cretaceous (145–66 mya). (Figs. 1.29,30)

Until recently, only one diving beetle genus, *Cretodytes* Ponomarenko, was known from the Cretaceous, but a number of dytiscid fossils are now being discovered from the early Cretaceous Yixian formation in China (Prokin and Ren, 2010; Prokin *et al.,* 2013). The fossils have been described in a number of new genera placed in the family Dytiscidae but *incertae sedis* in relation to extant subfamilies or in the extinct subfamily Liadytiscinae. It is noteworthy that not a single Mesozoic diving beetle fossil, neither Jurassic nor Cretaceous, has been placed in any of the extant 11 subfamilies. This may be due to the lack of a cladistic analysis that includes both extant and extinct species in combination with the shortage of clear diagnostic synapomorphies of subfamilies that are readily visible in ventral or dorsal fossil impressions. Some of these fossils from the Yixian formation are extremely well preserved, sometimes showing details of male genitalia or distinct elytral color patterns (Fig. 1.30; Prokin and Ren, 2010; Prokin *et al.,* 2013). Most of them are placed in the extinct Liadytiscinae based on the metacoxal plate/metasternal wing ratio, body length, shape of metacoxal processes, and length of metafemur and metatibia. But it is doubtful if any of these

Fig. 1.30. Early Cretaceous fossil Dytiscidae, *Mesodytes rhantoides* Prokin, Petrov, Wang, and Ponomarenko (2013), from the Yixian formation China. *Mesodytes* is classified in the extinct subfamily Liadytiscinae. Scale = 10.0mm.

characters prevent members of Liadytiscinae from actually belonging to an extant subfamily.

Paleogene-Neogene (66–2.6 mya). (Fig. 1.29)

In the Paleogene and Neogene periods the diving beetle fossils can generally be placed in extant subfamilies and often extant genera. A fossil from the Miocene Barstow formation, Southern California, was placed in the Vatellini tribe of hydroporines (Miller and Lubkin, 2001), and there are well-preserved fossils of elytral pieces from the Miocene that can unambiguously be placed as cybistrines, *Dytiscus* and *Colymbetes*, for instance. Four fossil diving beetles have been described from amber and deserve special attention, as amber-preserved fossils often show a high degree of details and characters. Two species of the genus *Copelatus*, *C. aphroditae* Balke and *C. predaveterus* Miller, were described from Baltic amber (Miocene) and Dominican amber (Miocene-Oligocene), respectively (Miller and Balke, 2003). The latter could be assigned to the *C. trilobatus* species group with 11 discal and 1 submarginal elytral stria. *Copelatus aphroditae* had 19 discal striae anteriorly and does not fit into any extant species group of *Copelatus* (Miller and Balke, 2003). The age of Baltic amber is debated, between 33 and 50 million years old, but this fossil at least puts the extant genus *Copelatus* into the Eocene. The same can be said for the genus *Hydroporus* after the description of *Hydroporus carstengroehni* Balke, Beigel, and Hendrich from Baltic amber (Balke *et al.,* 2010). This well-preserved specimen provided detailed characters of male tarsal adhesive setae, metacoxal processes, and punctuation and could unambiguously be placed in the extant Holarctic genus *Hydroporus*. These amber fossils represent two species-rich, widespread, and common genera of diving beetles. More surprising was the description of the rare, hygropetric agabine genus *Hydrotrupes* from Baltic amber (Gómez and Damgaard, 2014). *Hydrotrupes prometheus* Gómez and Damgaard is based on a very well-preserved specimen, and the affiliation with *Hydrotrupes* can hardly be disputed. It also indicates that the current distribution of *Hydrotrupes* in North America and China is a remnant of a historically larger distribution. The Baltic amber fossils include the oldest records of the subfamilies Copelatinae, Hydroporinae, and Agabinae to date. But as they can all be placed in extant genera, it is clear that the subfamilies must be much older still.

Quaternary (2.6 mya to present). (Fig. 1.29)

Quarternary fossils or subfossils of diving beetles are rather common in lacustrine sediments, bogs, fens, and mires. The subfossil fragments from the Holocene and late Pleistocene, commonly extracted from drill cores, can often be identified to extant species (e.g., Lemdahl, 1997; Lemdahl *et al.,* 2014). They are used to reconstruct past climate and changing aquatic nutrient environments. The northerly circumpolar species *Colymbetes dolabratus* (Paykull), for instance, is known from Denmark and Britain only as late glacial subfossils (Nilsson and Holmen, 1995; Buckland and Buckland, 2012) and bears witness of the colder climate in the recent past.

Collecting and Curating

As evident from the preceeding section, diving beetles can be found in many aquatic habitats, and different habitats may require different collecting techniques to fully investigate their diversity. A standard, heavy-duty D-net-style aquatic net (Figs. 1.31,33) is often best for marshes, streams, and other large habitats. The net is dragged or pushed through the vegetation or over the substrate, often multiple times, to disrupt the beetles (Fig. 1.31). The mesh of the net must be small enough to catch the smallest beetles, but not so small that debris clogs the net, which results in water pushed ahead of the net rather than through it. Many large beetles are able to outswim the net, particularly if it is clogged with debris, and can be collected better with a larger-diameter mesh, though at a potential loss of smaller

Fig. 1.31. Collecting with an aquatic net.

Fig. 1.32. Collecting a small rock pool with a kitchen strainer and white pan. Photo by R. Bukontaite. Used with permission.

Fig. 1.33. A heavy-duty D-frame water net with compartmentalizable shaft for packing and a white pan.

specimens. Small habitats such as puddles, margins of larger water bodies, rock pools, or tree holes can be most efficiently collected using smaller aquarium nets or kitchen strainers (Figs. 1.32,35). When hand-

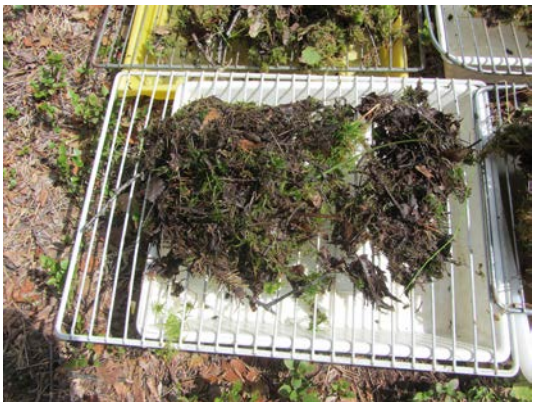


Fig. 1.34. White pan and screen extraction of specimens from debris collected in aquatic net.

Fig. 1.35. Kitchen strainers of different sizes are indespensable for small water holes that can be rich in diving beetles but where a full-size water net is too clumsy.

collecting dytiscids, larger specimens can be picked up with the fingers and placed into a collecting container, but an aspirator, a pipette, and "feather-tip" forceps are useful for picking up smaller specimens.

These techniques often result in considerable amounts of debris being collected in the net along with diving beetle specimens, which can make finding specimens in the net, especially small ones, difficult. To help with this, the detritus can be placed into a white pan to better see the beetles moving around (Figs. 1.32,33). A modified Berlese device can be used whereby the material in the net is deposited on a large screen placed on a light-colored collection container (Fig. 1.34). The specimens escape downward through the debris and land on the container, where they can be collected more easily.

An effective technique for trapping diving beetles, particularly larger specimens and larger species, is "bottle-trapping" or "minnow-trapping" (Hilsenhoff, 1987; 1991). Commercially available minnow or crayfish traps are effective (Figs. 1.36,37), and a bottle trap can be easily and inexpensively made from a soda bottle with the top cut

Fig. 1.36. Standardized bottle traps, crayfish traps, and bait.

Fig. 1.37. Crayfish ("dytiscid") trap in pond.

Fig. 1.38. Standardized bottle trap (*left*), set in pond (*right*).

off and inverted, making a funnel leading into the bottle. A more elaborate model based on two soda bottles (Figs. 1.36,38) has been used as standard for inventorying the two diving beetle species *Dytiscus latissimus* Linnaeus and *Graphoderus bilineatus* (DeGeer) protected under the European habitat directive. These traps are submerged in a shallow area of a pond, where diving beetles swim into the trap through the funnel, but once inside they find it difficult to swim back out. These traps can be baited with meat or other products, or improved either by using a light shining on the trap or by placing a "snap-

Fig. 1.39. Collecting at light by a leaf-choked forest pond.

Fig. 1.40. Collecting at light with vertical and horizontal sheets.

light" inside the trap itself. Traps such as these can be self-baiting as well, since, as individuals occur or die inside the trap, other specimens are attracted. For live trapping it is important that part of the trap rises above the water, allowing trapped specimens to surface and replenish their air supply (Fig. 1.38).

Many diving beetles fly at night and are attracted to ultraviolet (UV), mercury vapor, or aquarium lights, usually those that emphasize UV wavelengths. A white sheet with a light will attract specimens that can be collected off the sheet (Figs. 1.39,40). They often come in large numbers to such a device, and sometimes a different species diversity may come to a light than are collected using other methods in a given area. That said, often the specimens collected at a light are a subset of the diversity collected during the day using other methods.

Other habitats require alternative techniques. Hygropetric habitats can be hand-collected (Fig. 1.41), brushed with a scrubbing brush into a collecting screen (Fig. 1.42), or, especially on vertical surfaces, fogged with a weak insecticide, thereby agitating the beetles and causing them to emerge from hiding. They can also be collected by hand at

Fig. 1.41. Collecting a hygropetric habitat.

Fig. 1.42. Collecting using scrubbing brush and net material. Photo by Andrew E.Z. Short. Used with permission.

night by visually inspecting the surface with a light and aspirating specimens. Subterranean taxa are collected by dropping a collecting net into a well or borehole to strain the specimens from the water. In other cases, subterranean diving beetles wash out of streams or well pumps, where they can be collected using drift nets (Fig. 1.43), and cave species may be hand-collected if caves can be entered (Fig. 1.44). Hyporheic species require boring into the substrate and straining specimens from water collected in the hole. Terrestrial specimens have been collected using Berlese or Winkler devices to extract leaf litter. Bromeliad and other phytotelmatic species require dissection of the plant material or pouring the water out of the container through a strainer.

Diving beetle adults can be collected into ethanol or a kill jar charged with ethyl acetate or cyanide. They can be permanently preserved in ethanol. High-concentration ethanol (e.g., 96%) will make beetles more brittle than lower concentrations (70%–80%), but higher concentrations may be required for DNA preservation. Specimens are difficult to identify to species when examined in alcohol since features such as surface sculpture are

Fig. 1.43. Drift net at emergence of spring.

Fig. 1.44. Collecting in a cave, Madagascar. Photo N. Apelqvist. Used with permission.

obscured. Specimens should be removed from the ethanol and dried to identify, after which they can be returned to the alcohol for storage, if desired. Many traditional preparators, especially in parts of Europe, glue specimens to cards (Fig. 1.45c). Although this certainly helps protect the specimen, it has the disadvantage of obscuring an entire surface of the beetle, most frequently the ventral surface, where many of

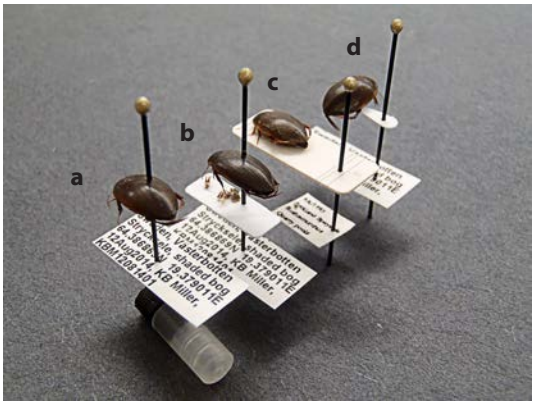


Fig. 1.45. Alternative techniques for mounting specimens. **a**, Pinned specimen with genitalia in microvial. **b**, Pinned specimens with genitalia glued to card. **c**, Card-mounted specimen. **d**, Point-mounted specimen.

the most critical diagnostic characters are located. Pinning (Fig. 1.45a) or pointing (Fig. 1.45d) is more effective in allowing examination of the specimen, though it makes it more vulnerable to damage. Immature life stages (larvae and pupae) should be collected into a fixative such as Kahle's fluid or fixed in boiling water and then stored in 70%–80% ethanol. They can be cleared in potassium hydroxide (KOH), stained, and slide mounted as well.

Adult male genitalia are often critical for identification of diving beetle species and sometimes groups of species. These are dissected by extracting the genital capsule from a fresh or relaxed beetle from the abdominal apex. Diving beetles are robust and can be easily relaxed by placing them briefly into near-boiling water. A fine pair of forceps or a hooked pin or probe can be used to reach into the end of the abdomen along the side and grasp or hook the base of the aedeagus. Once removed, the structures can then be teased apart with sharp forceps or probes in alcohol or water. The structures can then be mounted on a card and attached to the pin with the specimen (Fig. 1.45b) or placed in a genitalia vial and attached to the pin (Fig. 1.45a). Female genitalia are often important for characterizing certain taxa, but are somewhat more difficult to prepare than male genitalia. The most effective technique for examining sclerotized and membranous portions of the female reproductive tract is to remove the entire abdomen, or the entire apex with the genital capsule included, and to place these structures together in hot 10% KOH for several minutes. The KOH will macerate the soft tissues. The structures can then be removed from the KOH, rinsed and placed in a dye, such as Chlorozol Black, to stain the structures for more careful dissection and examination. They can then be stored in glycerin in a genitalia vial attached to the pin or slide mounted.

Diving Beetles and Human Society

Conservation.

Many diving beetle species and populations have likely been influenced by human activities. In many cases, diving beetle populations have probably been enhanced by humans, since people often introduce or maintain water in many areas that naturally have water only rarely, such as stock tanks or reservoirs in desert regions. Other species, however, have likely been influenced negatively by humans through habitat changes such as degradation of stream shorelines, draining and altering of wetlands, introduction of fish and other species, and other activities such as use of pesticides (perhaps especially in the control of mosquitoes) (e.g., Heckman, 1981), though relatively little is known of these effects. A few species may have been artificially introduced to new geographic regions (Leech, 1970), though this does not seem to have been common. In some cases, particular species have been negatively influenced by other human activities, such as introduction of competing animal species (Bameul, 2013).

A great many diving beetle species are extremely rare in collections with many known only from single specimens or from a single location. This is true of many epigean species, and particularly true of terrestrial, subterranean, hyporheic, or hygropetric ones. Because of this, it is difficult to assess whether species are, in some meaningful way, vulnerable or endangered, or simply poorly collected. A number of species are of conservation concern, however, with numerous diving beetles on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species. Many of these are species with much better historical knowledge of their declining population sizes through time. Diving beetle conservation was reviewed by Foster and Bilton (2014).

Applied entomology.

Diving beetles may be useful indicators of water or wetland quality, or of toxins or other environmental concerns (e.g., Foster, 1996; Painter, 1999; Mebane *et al.*, 2012). Together with other aquatic beetle families, several studies promote their usefulness as indicators of biodiversity and as a tool for selecting areas worthy of conservation (Sánchez-Fernández *et al*., 2004; 2006; Foster and Eyre, 1992; Foster *et al.*, 1990; Ribera and Foster, 1992; Dong *et al.*, 2014). As aquatic, air-breathing, generalist predators, typically in marginal, small habitats, their general utility in this regard may be somewhat limited. They may be more important in their role as predatory pests in fish-farming contexts (Wilson, 1923). They may also be important biological control agents for medically important taxa such as mosquitoes (Lundkvist *et al.*, 2003; Culler and Lamp, 2009). Finally, their complex chemistry may eventually provide useful compounds for human activities, but this has been barely investigated (Dettner, 2014).

Human culture.

Diving beetle adults are used as food by people in some regions, especially eastern and southeastern Asia (De Foliart, 2002; Jäch, 2003). Some, like certain *Cybister* species, are actually farmed for consumption (Jäch, 2003). Apparently, there is an ancient history of their use as food. Specimens of *Cybister explanatus* LeConte (without their heads) were found in prehistoric human coprolites in a cave in Nevada (Roust, 1967). Many other components of the coprolites were characteristic of the Humboldt Sink (fish, mussels, etc.) (Roust, 1967), suggesting the aquatic beetles probably also came from that site.

Diving beetles occasionally appear in other areas of human culture. For example, they sometimes enter into creation stories. An Amerindian Cherokee creation narrative has a diving beetle traveling from the sky realm to see what was in the expanse of water, or "liquid chaos" (Powell, 1900). He found nowhere to rest, so he brought soft mud up from the bottom that spread out into the land forming the entire earth (Powell, 1900). Remarkably, in areas of eastern Africa, young girls collect diving beetles that are induced to bite the nipples, which is thought to stimulate breast growth (Kutalek and Kassa, 2005). Diving beetles have occasionally appeared on postage stamps or even coins, and some (e.g., the "sunburst diving beetle," *Thermonectus marmoratus* (Gray) or *Cybister fimbriolatus* (Say)) are often included in "insect zoos" (Morgan, 1992).

2. Taxonomy and Morphology

Methods

Scope.

The focus of this work is the Dytiscidae fauna of the world at the genus- and family-group ranks of the adult life stage. Keys are provided for all genera, subtribes, tribes, and subfamilies. Subgenera have been described for several groups, and these are treated less formally in the genus treatments. The egg, larval, and pupal life stages are not comprehesively treated, but references are made to descriptions of these life stages if they are available, the general morphology of these life stages is described, and a key to the subfamilies based on the larvae is provided.

Body length.

The known range of body lengths is provided based on published records compiled by A. N. Nilsson (pers. comm.).

Diagnoses.

Complete taxon descriptions are not provided. Instead, emphasis is placed on major diagnostic features (including illustrations) allowing for identification. References are provided for more complete treatments of diversity in the groups.

Subterranean taxa present a special problem since they are highly convergent in loss of eyes, depigmentation, reduced flight wings, and body shape. They look more similar to each other than to their nearest relatives (see Fig. 3.51). For this reason, known subterranean taxa are keyed separately. The genus treatments, however, are included in the tribes and subfamilies to which they belong.

Classification.

A comprehensive catalog of all names in Dytiscidae is available (Nilsson, 2001; 2003c; 2004; 2015; 2016; Nilsson and Fery, 2006). The nomenclature in this volume follows that catalog. Valid names, authors, and dates of publication are based on the catalog and literature review for the past few years. The taxonomic scheme used here follows a recent higher phylogenetic classification developed by Miller and Bergsten (2014a). No new taxonomic changes are made relative to the catalog, apart from a few cases of taxonomic changes published or in press in 2016, and only a limited review of invalid names or obsolete concepts is made in the review of each taxon. One exception is our use of the Hygrotini genus-group name *Coelambus* at the genus rank instead of subgenus (of *Hygrotus*), but this is consistent with many historical authors.

Diversity.

The number of species for each taxon follows the electronic updated world catalog of Dytiscidae (Nilsson, 2016), including species described up until 31 December 2015, except a few cases where taxa described or in press in 2016 are included. When revisions or reviews exist, these are referenced.

Natural history.

Brief reviews of the habitat or life history of members of each genus are provided when information is available, along with references to the information. The natural history of the great majority of species and larger groups is extremely poorly known, and, in many cases, only limited information is available.

Distributions.

Generalized distribution maps are provided for each genus based on literature review and examinations of specimens by the authors. Distributions for some groups and some regions are much better known than others. For some genera, the known distribution is very limited and probably extends much beyond the indicated range on the map. This is particularly true of taxa in Southeast Asia, central Africa, and South America, each of which have large numbers of taxa known from few specimens. In other cases, a region may include many widespread taxa, but their distribution limits are poorly known. This is particularly true of taxa occurring in northern North America, Siberia, South America, and central Africa. Therefore the distribution maps are primarily estimates. It will be unsurprising if taxa are eventually found outside the range limits indicated or found

to be more regionally limited within these ranges as collection effort improves.

Illustrations.

A goal of this project is comprehensive illustration of diagnostic features of diving beetles. Line drawings are provided for most features used in keys and diagnoses, and photographic images are provided for others. A photograph of the habitus is provided for at least one representative of all genera except *Sinodytes*, which is known from a single specimen of a single species, and the type specimen was not located and may be lost. For larger or more diverse genera, more than one photo is provided. Photographs by the authors were acquired using a Visionary Digital BK Plus Lab Imaging System (R. Larimer, www.visionarydigital.com) and a Stackshot (www.cognisys-inc.com) rail-mounted Canon EOS 5D Mark II DSLR camera with macrolenses together with the stacking software Zerene stacker (www.zerenesystems.com). Photos were extensively postedited in Adobe Photoshop. In some cases, photographs were acquired by colleagues, and these are attributed. In all other cases, illustrations are original productions by the authors. Line drawings were sketched using a dissecting scope with a drawing tube and inked in Adobe Illustrator.

Diagnosis and Relationships of Dytiscidae

Diving beetles belong to the beetle suborder Adephaga and exhibit the typical adult characteristics of that group, including a large, external propleuron and visible notopleural suture (Fig. 2.6b), and a first visible abdominal ventrite (second abdominal sternum) that is distinctly divided by the metacoxae (Fig. 2.6b). Also, the metatrochanter is large and distinctly offset from the line of the metafemur (Fig. 2.6b), the 11-segmented antennae are filiform in most species (Fig. 2.6, some have the antennae clubbed or medially expanded or modified in males, Fig. 2.7m), and the tarsomeres number 5-5-5 (Fig. 2.6, though Hydroporinae have pro- and mesotarsomere IV reduced, and a few have only three or four protarsomeres in males, Fig. 2.11e,f). Diving beetle adults have paired pygidial glands like other Adephaga, and the metacoxae are immobile and fused medially. Larvae are also typical of Adephaga with the labrum and clypeus fused, no mandibular mola, six-segmented legs, four antennomeres, and articulable urogomphi. Monophyly of Adephaga is not in doubt, with many additional features that associate the families, including Dytiscidae (Beutel and Ribera, 2005)

The family Dytiscidae is monophyletic but exhibits relatively few distinctive characteristics. Adults have prothoracic defensive glands anterolaterally in the prothorax, which is unique in Adephaga. Paelobiidae also have prothoracic glands, but they are structured and positioned differently in the prothorax (Forsyth, 1968; 1970; Balke *et al.*, 2005; Beutel and Leschen, 2005; Dettner, 2014). Diving beetles also have the metacoxa strongly expanded anteriorly into a prominent lobe with the anterior margin distinctly curved (Fig. 2.1a), whereas in other families the anterior margin of the metacoxa is not so expanded and is relatively straight (Fig. 2.1b). In other respects, adult diving beetles are quite variable and not easily diagnosed with respect to other aquatic adephagan groups. Larvae have an eight-segmented abdomen, the antennae typically well developed, the legs natatory or ambulatory, two claws on the pretarsus, and the spiracles on abdominal segment VIII located apically or apicoventrally. Finally, dytiscid adults swim with simultaneous movements of the metathoracic legs like Noteridae, but unlike Paelobiidae and Haliplidae, which use alternating movements of the legs, and unlike Amphizoidae, Meruidae and Aspidytidae, which do not swim.

There is, as yet, no clear consensus on the relationships among extant Adephaga families. There is some evidence that the aquatic families, including Dytiscidae, comprise a clade called Hydradephaga (as distinct from Geadephaga, which includes the terrestrial Carabidae and Trachypachidae) (Crowson, 1955; 1960; Burmeister, 1976; Baehr, 1979; Ruhnau, 1986; Shull *et al.*, 2001). Within Hydradephaga, if it is monophyletic, relationships among families are also not clear, especially with respect to Haliplidae and Gyrinidae, but it is generally thought that the families Noteridae, Aspidytidae, Amphizoidae, Paelobiidae, and Dytiscidae form a clade called Dytiscoidea (Bell, 1966; Beutel and Haas, 1996; 2000; Beutel, 1998; Ribera *et al.*,

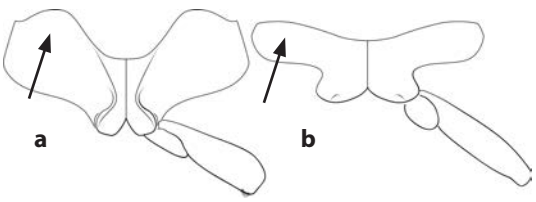


Fig. 2.1. Hydradephaga metacoxae and left metatrochanter and metafemur. **a**, *Agabus obliteratus*. **b**, *Amphizoa insolens* (Amphizoidae).

2002a; b), likely also including Meruidae (Beutel *et al.,* 2006; Balke *et al.,* 2008; Dressler *et al.,* 2011; but see Alarie *et al.*, 2011b; Short *et al.,* 2012; Toussaint *et al.,* 2015). Dytiscidae is probably most closely related to Paelobiidae, and, more distantly, to Amphizoidae and Aspidytidae (Ribera *et al.*, 2002a; Beutel *et al.,* 2006), but molecular data have given various results, none of them with strong support (Balke *et al.,* 2005; 2008; Toussaint *et al.,* 2015). All studies agree, however, that Noteridae and Meruidae are the most distantly related dytiscoids to Dytiscidae.

History of Systematic Study

Diving beetles are common elements of the European aquatic insect fauna and, as such, were included in many early works that seeked to discover the natural system of insects. The 10th edition of the *Systema Naturae* (Linnaeus, 1758) included *Dytiscus* Linnaeus in Coleoptera. Numerous new species were described during the late 1700s and 1800s in major regional treatments and more isolated species descriptions. Several investigators, however, stand out for more comprehensively treating the group during this time, including Aubé (1838), Crotch (1873), Sahlberg (1873), and Régimbart (1879).

The most significant advance in the history of diving beetle taxonomy based on an early understanding of phylogenetic classification was by the great British coleopterist David Sharp (1882). In an immense masterpiece, he included about 1,140 species, many of which are still valid, though his higher groups, in general, have been shown to be largely unnatural (not monophyletic). He tended to emphasize only one or a few characters for hypothesizing relationships and had a view of evolutionary advancement to "perfection" that we do not generally subscribe to today. Nevertheless, even given the limitations of theory and practice of the time, there is no denying Sharp's incredible contribution to knowledge of dytiscid diversity, and his work on Hydradephaga remains influential even to this day.

The next 100 years was marked by the addition of great numbers of new species and genera, largely within the context of Sharp's (1882) higher classification. Strongly influential workers active during this period included Maurice Régimbart (1895; 1899) (contemporary with David Sharp), Alois Zimmermann (1919; 1920; 1930; 1931; 1933; 1934) and his posthumus coauthor, Leopold Gschwendtner (Zimmermann and Gschwendtner, 1935; 1936; 1937; 1938; 1939), and Félix Guignot

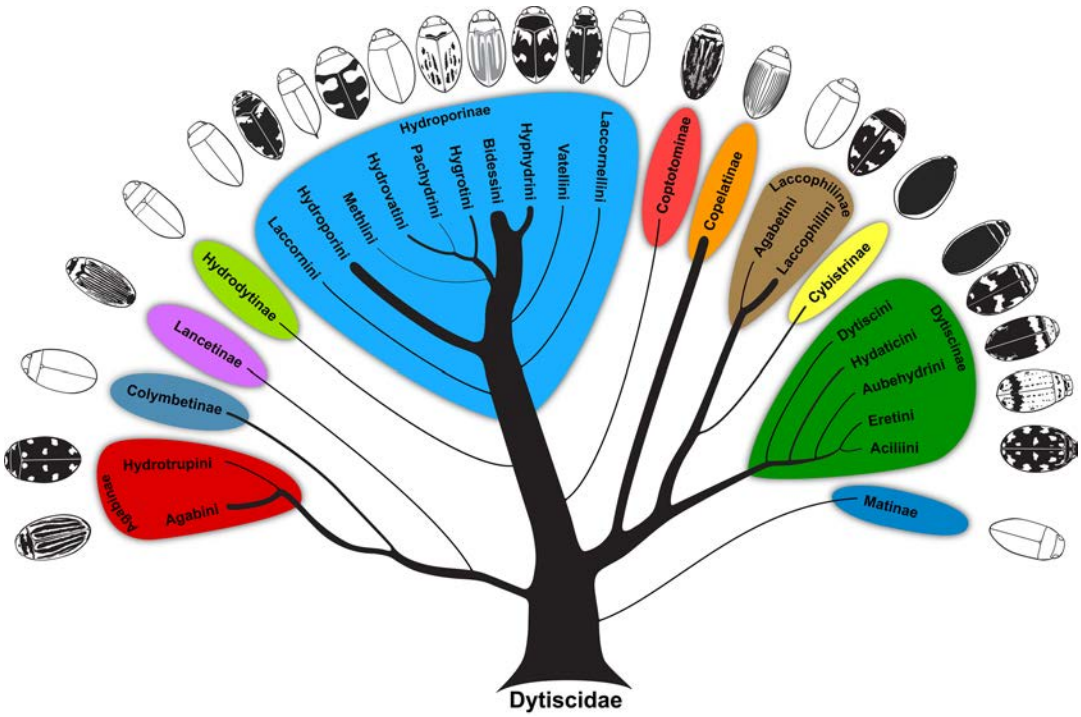


Fig. 2.2. Phylogeny of Dytiscidae from Miller and Bergsten (2014b). Branch sizes are proportional to fraction of total Dytiscidae species in that branch.

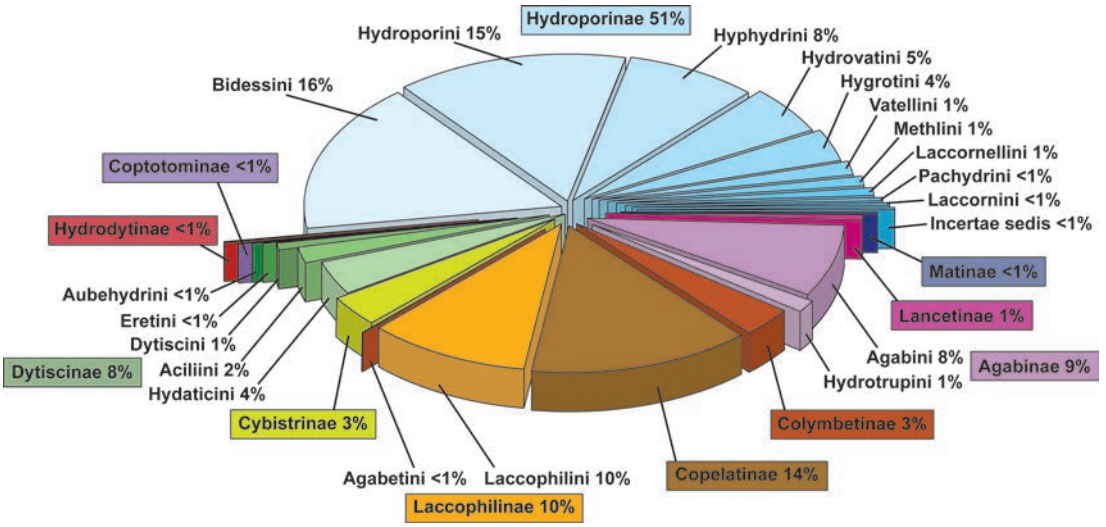


Fig. 2.3. Family groups of Dytiscidae showing percentage of species included in each group.

(1947; 1959a; b; 1961), each of whom also had numerous smaller works. Sharp and Régimbart together described 71% of the new Dytiscidae names from 1870 to 1909, and Zimmermann and Guignot introduced 50% from 1910 to 1961 (Nilsson, 2008).

Modern (cladistic) development of diving beetle phylogenetic classification began especially with Ernst-Gerhard Burmeister (1976), who was strongly influenced by Willi Hennig and focused especially on characters of the female reproductive tract (Burmeister, 1976; 1980; 1990). His work resulted in removal of *Agabetes* from Colymbetinae to Laccophilinae and elevation of Copelatini out of Colymbetinae into its own subfamily. Other major cladistic analyses of higher taxa during this period were those by G. William Wolfe (1985; 1988), Rolf Beutel (1993; 1994; 1995), and Stefan Ruhnau (1986) and Ruhnau and Michel Brancucci (1984), who refined the classifications of several groups, including removal of *Lancetes* from Colymbetinae into its own subfamily and internal tribal rearrangements of Hydroporinae, based on morphology. Beutel and Robert Roughley (1987) presented convincing evidence that Noteridae are not dytiscids (with Amphizoidae and Paelobiidae closer to Dytiscidae than Noteridae), and few workers since have continued to recognize noterids as a dytiscid subfamily.

Kelly Miller (2000; 2001c) summarized many of the known morphological data and conducted a major cladistic analysis and revision of the higher dytiscid classification. His work included synonymy of Aubehydrinae with Dytiscinae (Miller, 2000) and formal elevation of Copelatinae, Coptotominae, Matinae, and Agabinae from tribes within Colymbetinae *sensu auctorum* (Miller, 2001c). A new subfamily, Hydrodytinae, was also erected (Miller, 2001c; 2002b). More recent developments have included molecular (Ribera *et al.*, 2002b; 2008) and combined analyses of various groups (e.g., Miller, 2003; Balke and Ribera, 2004; Ribera *et al.*, 2004; Miller *et al.*, 2007b; 2009a). A comprehensive phylogeny of major groups using morphology and several genes was done by Miller and Johannes Bergsten (2014a), and the classification presented here is based on their conclusions (Fig. 2.2).

Additional modern developments in dytiscid systematics include discovery of large numbers of new species with over 4,300 valid species now known (Nilsson, 2003c; 2004; 2008; 2015; 2016; Nilsson and Fery, 2006), though Nilsson-Örtman and Nilsson (2010) predicted about 5,400 total world species. Many large genera (e.g., *Copelatus*, *Laccophilus*) have not been well revised and probably have a lot of new species. New taxa in subterranean, phytotelmatic, hygropetric, and terrestrial habitats will probably add to total dytiscid diversity. Also, knowledge of larvae has accelerated rapidly largely because of intensive and excellent work by Yves Alarie, Mariano Michat, and collaborators (e.g., Alarie and Harper, 1990; Alarie *et al.*, 1990a; 1997; 1998; 2000; 2001b; 2002a; b; 2011a; Alarie, 1995b; 1998; Alarie and Butera, 2003; Alarie and Hughes, 2006; Alarie and Michat, 2007). Finally, a comprehensive catalog of all dytiscid names developed mainly by the exceptionally careful work of Anders N. Nilsson has stabilized the nomenclature and solved many of the problems with dytiscid names to reflect the best, most recent phylogenetic conclusions (Nilsson, 2001; 2003c; 2004; 2015; 2016; Nilsson and Fery, 2006). The last world cata-

log was by Zimmermann (1920), which is well out of date.

The classification presented here (Fig. 2.2) based on Miller and Bergsten (2014a), includes 11 subfamilies, 19 tribes, and 4 subtribes. By far, the largest group is Hydroporinae with over half of all species and with numerous tribes. Of these, Bidessini, Hyphydrini, and Hydroporini are very large, together accounting for about 39% of known species. Copelatinae, Laccophilini, and Agabini together account for another 32% of all species with the remaining groups much less speciose (Fig. 2.3).

Dytiscidae Morphology

The morphology and taxonomy reviewed here emphasize adults, mainly diagnostic character systems important in the classification and identification of the taxa. Also emphasized are external, sclerotized, or membranous "hard parts," though some internal structures, like the metafurca and the proventriculus, are briefly described. Soft tissues have been studied (musculature, gland structure, midgut, etc.), but these are not routinely examined in diving beetle systematics and are not included here. A review of larval morphology was presented by Larson *et al.* (2000), and morphology of larvae, especially diagnostic features, is briefly reviewed here. Eggs and pupae have been little studied, unfortunately.

Eggs

Eggs of diving beetles have not been well described (Hinton, 1981). The eggs are typically small, white to light brown, oval, and similar across the group, which is usual for Coleoptera.

Larvae

Diving beetles have three larval instars. Although Nicolai and Droste (1984) suggested the presence of four instars in a species of *Lancetes*, this was convincingly disputed by Alarie *et al.* (2002a), who asserted that *Lancetes* have only three. Instar I can generally be distinguished from II and III by the presence of spinous egg-bursters on the posterior portion of the frontoclypeus (Fig. 2.4a, though absent in Cybistrinae). Instar III can usually be distinguished by the presence of spiracles laterally on the meso- and metathorax and abdominal segments I–VII. A few taxa (e.g., *Heterosternuta* and *Neoporus*),

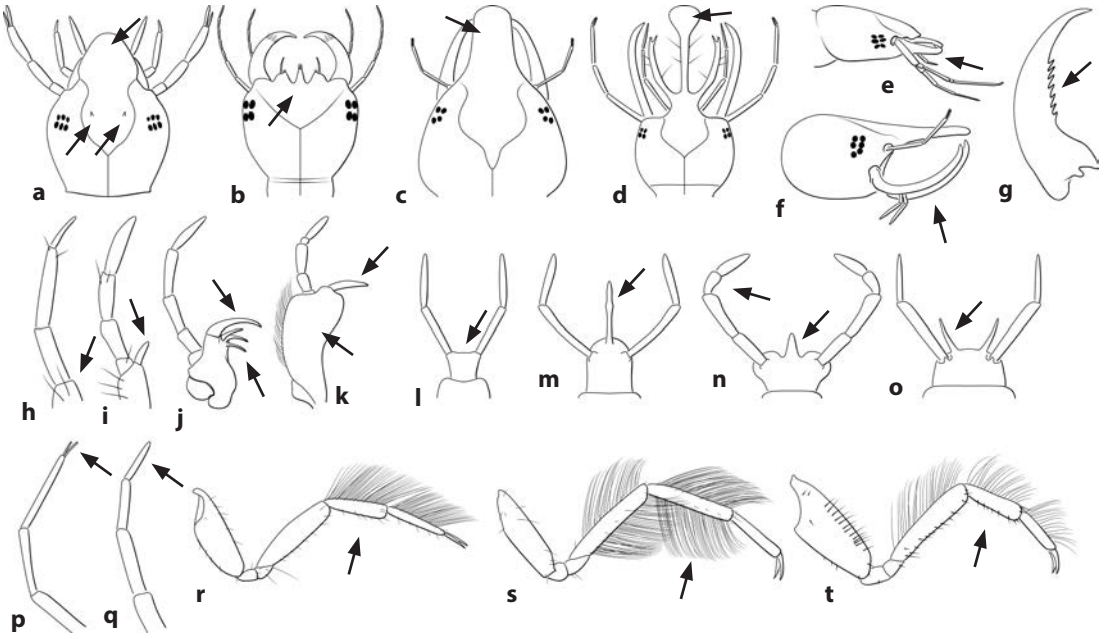


Fig. 2.4. Dytiscidae larvae. **a**, *Hydroporus* sp. first instar head. **b**, *Megadytes* sp. head. **c**, *Hydrovatus pustulatus* head. **d**, *Vatellus* sp. head. **e**, *Dytiscus marginalis* head, lateral. **f**, *Hydrovatus pustulatus* head, lateral. **g**, *Copelatus* sp. mandible. **h**, *Neoporus* sp. maxilla. **i**, *Rhantus* sp. maxilla. **j**, *Copelatus* sp. maxilla. **k**, *Graphoderus* sp. maxilla. **l**, *Hydroporus* sp. labium. **m**, *Graphoderus* sp. labium. **n**, *Megadytes* sp. labium. **o**, *Hydaticus* sp labium. **p**, *Laccophilus* sp. antenna. **q**, *Matus* sp. antenna. **r**, *Neoporus* sp. metathoracic leg. **s**, *Dytiscus dauricus* metathoracic leg. **t**, *Rhantus binotatus* metathoracic leg.

however, lack spiracles in instar III. In these cases, and with Cybistrinae, cranial measurements and the presence of a number of other specific features may be important for distinguishing among the instars.

Setae and pores (chaetotaxy and porotaxy) of the various larval body regions have been used

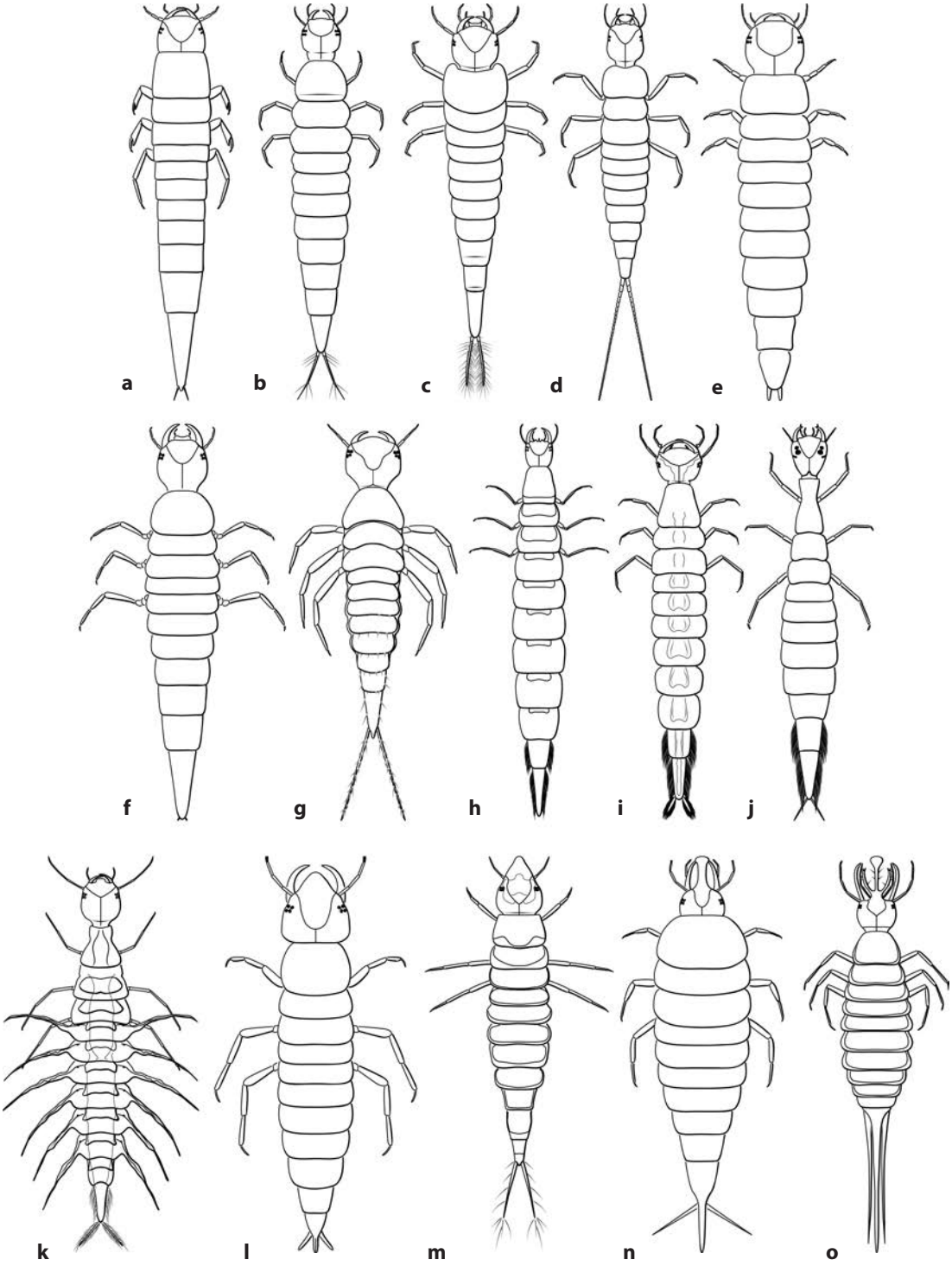


Fig. 2.5. Dytiscidae larvae. **a**, *Matus bicarinatus*. **b**, *Agabus* sp. **c**, *Rhantus suturalis*. **d**, *Lancetes* sp. **e**, *Copelatus* sp. **f**, *Agabetes acuductus*. **g**, *Laccophilus* sp. **h**, *Megadytes* sp. **i**, *Dytiscus dauricus*. **j**, *Acilius* sp. **k**, *Coptotomus* sp. **l**, *Celina* sp. **m**, *Neoporus* sp. **n**, *Hyphydrus ovatus* **o**, *Vatellus* sp.

extensively in larval diagnostics and phylogenetics during recent years. Chaetotaxy of instar I (primary sensillae, pores, and setae), in particular, is highly conserved across the group, and variation in its form is particularly useful for documenting relationships. Instars II–III often exhibit considerable addition of pores and setae (secondary sensillae, pores, and setae), which are also useful, in general, for diagnostics and relationships.

Head.

The cranium is typically more sclerotized than much of the rest of the body. It varies in shape with some species quadrate, others rounded, and others triangular. The frons and clypeus are fused into a frontoclypeus. The dorsal surface of the head is characterized by the Y-shaped epicranial suture, which delimits a medial frontoclypeus and lateral epicrania. In some cases there is a posterior occipital suture. Ventrally, the cranium has a distinctive gula.

The anterior margin of the frontoclypeus is often modified. Members of Cybistrinae, for example, are distinctly trilobed with the lobes often spinous and variously developed (Fig. 2.4b), depending on species. Hydroporinae have the anterior margin strongly projecting anteriorly into a variously modified "nasale," which may be elongate, apically lobed or expanded, or otherwise modified in various ways (Figs. 2.4c,d,2.5l–o). The labrum is fused with the clypeus, as in other Adephaga.

The six stemmata are located laterally (Fig. 2.4a–f). Larvae of subterranean taxa often lack stemmata entirely. Members of Eretini and Aciliini have the anterodorsal and mediodorsal stemmata distinctly enlarged, and members of Dytiscinae have an additional, rudimentary light-organ posterad to the posterodorsal stemmata.

Mouthparts. The mandibles are elongate and falcate (Fig. 2.4e,f). They are used in extraoral digestion using a medial channel or groove through which saliva and fluids from prey items are passed. In many taxa the mandibles are horizontal (Fig. 2.4e), but in Hydroporinae they are curved dorsad and interface with the nasale (Fig. 2.4f). Known Copelatinae larvae have the mandibles serrated without a medial channel or groove (Fig. 2.4g) and, together with the presence of a crop, is evidence of solid-food, rather than liquid, feeding. Larvae of *Hydrotrupes* also lack a mandibular channel (Beutel, 1994; Alarie *et al.*, 1998).

Maxillae are typical for adephagan larvae. Dytiscids usually have a developed cardo, stipes, a palp with three segments and a basal palpifer, and galea (Fig. 2.4i). Some taxa (e.g., Laccophilinae, Copelatinae) have two to three curved, spine-like structures posterad to the galea, which may represent laciniae (Fig. 2.4j). The cardo and stipes are fused and there is no galea in Hydroporinae (Fig. 2.4h). Some taxa have secondary segmentation of the palpomeres in instars II and III or, in Cybistrinae, also in instar I. A few taxa have the maxilla broad and more complex, such as in Aciliini (Fig. 2.4k).

The labium has a developed prementum, postmentum (or mentum), and palps of three (a few Hydroporinae) or two (all other taxa) palpomeres (Fig. 2.4l–o). Members of Aciliini, Eretini, and Cybistrinae have a ligula on the prementum between the palps in different shapes (Fig. 2.4m,n), and Hydaticini have typically a pair of lobes (Fig. 2.4o). Instars II–III of *Dytiscus* and I–III of Cybistrinae have the palps subdivided into additional palpomeres.

Antennae. The antennae are typically filiform with four antennomeres (Fig. 2.4p,q). Antennomere III has a sensory process that may be short and inconspicuous to long, nearly as long as antennomere IV, making the antennae appear biramous apically (Fig. 2.4p). Instars II and III of some taxa (and instar I of Cybistrinae) have antennomeres further divided making the antennae with more than four antennomeres (Fig. 2.4b).

Thorax.

A distinctive, large prothoraxa and smaller meso- and metathorax make up the larval thorax (Fig. 2.5). Each segment has a distinctive tergum and small pleural sclerites. Most taxa have the venter membranous except a small prosternum on the prothorax. The terga have longitudinal ecdysial sutures. Instar III in most taxa has a pair of lateral spiracles on the meso- and metathorax (except, e.g., *Neoporus* and *Heterosternuta*).

Legs. Larval Dytiscidae have elongate, natatory, or ambulatory legs composed of five segments, typical of Adephaga. Tarsal claws are generally unequal in length. Instars II–III of many taxa have a series of long, natatory setae on the dorsal margin or both dorsal and ventral margins of the tarsi, tibiae, and (in some taxa) femora (Fig. 2.4r–t). An unusual modification to the legs is in some species of *Matus* that have the apical angles of the profemur and protibia extending ventrad under the protarsus forming a pseudochelate leg.

Abdomen.

The abdomen is elongate and composed

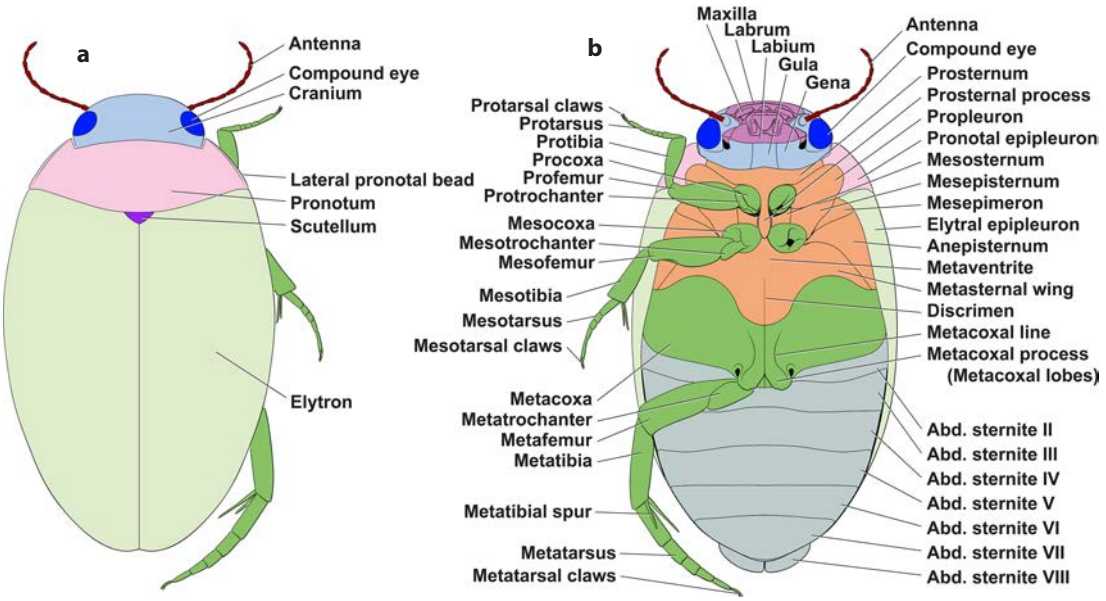


Fig. 2.6. Morphological features of Dytiscidae. **a**, Dorsal aspect. **b**, Ventral aspect.

of eight segments (Fig. 2.5). Segment VIII is modified for respiration and bears the apical urogomphi and a pair of spiracles (Fig. 2.5). Each segment has a tergal sclerite that extends laterally to the margins except Cybistrinae, in which the abdomen is nearly entirely membranous except for few small plates on each dorsum (Fig. 2.5h). Segment VIII is typically entirely sclerotized, and in some taxa VII and, more rarely (e.g., *Agabetes*), VI is entirely sclerotized. The tergum of segment VIII extends posteriorly beyond the base of the urogomphi and bears a pair of spiracles. This is called the siphon and it is extended into the atmosphere above the water line for respiration. Segments I–VII also each have a pair of lateral spiracles in instar III, though these are absent in all instars in some taxa (e.g., *Heterosternuta* and *Neoporus*). Segment VIII (Coptotominae) or VII–VIII (Dytiscinae, Cybistrinae) have a series of long, natatory setae along each lateral margin (Fig. 2.5h–j).

The urogomphi are each composed of one or two segments (e.g., Fig. 2.5b) or are multiannulated (Fig. 2.5g). They are strongly reduced in some taxa, such as Cybistrinae (Fig. 2.5h). The urogomphi may have only few (Fig. 2.5b) or many (Fig. 2.5c) setae, depending on the taxon. Members of Dytiscini have the urogomphi flattened and with a fringe of long, natatory setae along the margins (Fig. 2.5i).

Pupae

Pupae have been described for only a few species. Known pupae are exarate with a nine-segmented abdomen, though segment IX is small and bears a pair of urogomphi.

Adults

Body shape and size.

Dytiscids are usually streamlined, dorsoventrally flattened beetles with both the dorsal and ventral surfaces usually convex. However, there is substantial variation in body shape with some species elongate and relatively slender (e.g., Fig. 21.3) and others short and broad, or even nearly spherical (e.g., Fig. 34.4). The lateral outline may be nearly continuously curved (Fig. 2.6a) or distinctly interrupted between the pronotum and elytron (e.g., Fig. 8.9), particularly in rheophilic, hyporheic, or subterranean taxa. The head, prothorax, and elytra (the three portions of the body visible in dorsal view) vary in their relative sizes and shapes depending on the taxon.

Diving beetles are highly variable in size with some of the smallest and largest of all water beetles represented in the family. Size and relative size and shape are often used as taxonomic features. Greatest length is measured from the anterior margin of the clypeus to the elytral apices. Greatest width is measured across the body at its widest point. Often a ratio of length:width is used to describe the shape of a diving beetle with short, robust species often having very low ratios and longer, more slender species with higher ratios. Measurements and ratios of measurements of other features are also often used

for diagnostics and descriptions of diving beetles such as eye width compared with head width, length of antennae or length and width of specific antennomeres, width of the metasternal wing compared to the width of the metacoxae, relative length of the metafemur to length of the metatrochanter, and others.

Coloration.

Diving beetles have an impressive range of color and color patterns. Though many species are relatively uniformly colored (e.g., Fig. 9.16), many others are attractively marked with maculae (e.g., Fig. 13.20c), fasciae (e.g., Fig. 28.17), or stripes (e.g., Fig. 8.8b). Color and color patterns are useful for diagnostics of dytiscids, particularly at the species level, but color can be quite variable and is often best used in combination with a more thoroughgoing knowledge of other features, such as male genitalia. Coloration can be affected by the degree of natural variability within a species, age of specimens (with teneral individuals often more pale or with more demarcated or distinctive maculae), and, importantly, type of preservation. Some species have pigments that are lost after death or after use of certain preservation methods such as alcohol.

Cuticule sculpture.

Although dytiscids are usually smooth and streamlined for an aquatic lifestyle, they have an astonishing variety of surface sculpturing in the form of punctation, microreticulation, striae, rugae, and even setae, spines, and spurs. Usually these features are best examined in dried specimens that are relatively clean. Specimens in alcohol or that are greasy or dirty are difficult to examine for these features. Specimens are also best examined with proper lighting conditions, and often a diffuse, oblique light source is best for illuminating surface sculptures.

Larger surfaces — such as the cranium, pronotum, elytra, metaventrite, metacoxae and abdominal sterna — often have punctation that may be of different sizes and densities, depending on the taxon. In some cases, these punctures bear fine setae. These surfaces are also often covered with a microreticulation of fine, impressed lines that form cells of various sizes and shapes that are particularly useful for species diagnostics. In some cases the cells are round and small, in others larger and irregular in shape, and in others the lines are variously distinctive or obscured. In some cases, two types of sculpturing may be present along with punctation.

Head.

The diving beetle cranium is broadly inserted into the prothorax. The dorsal surface is dominated by a broad area comprising the vertex, frons, and clypeus. The clypeal suture is only visible laterally (Fig. 2.7b–g) except in *Dytiscus*, which have a complete clypeal suture (Fig. 2.7a). Ocelli are absent, but the compound eyes are typically large to very large and located around the lateral surface of the cranium. Some rheophilic taxa have reduced eyes, and many subterranean taxa have the eyes strongly reduced or absent (see Fig. 29.6). The anterior margins of the compound eyes are usually emarginate (Fig. 2.7b), but in Cybistrinae and Dytiscinae are evenly rounded anteriorly and produced (Fig. 2.7a). The ventral part of the cranium is narrowed,

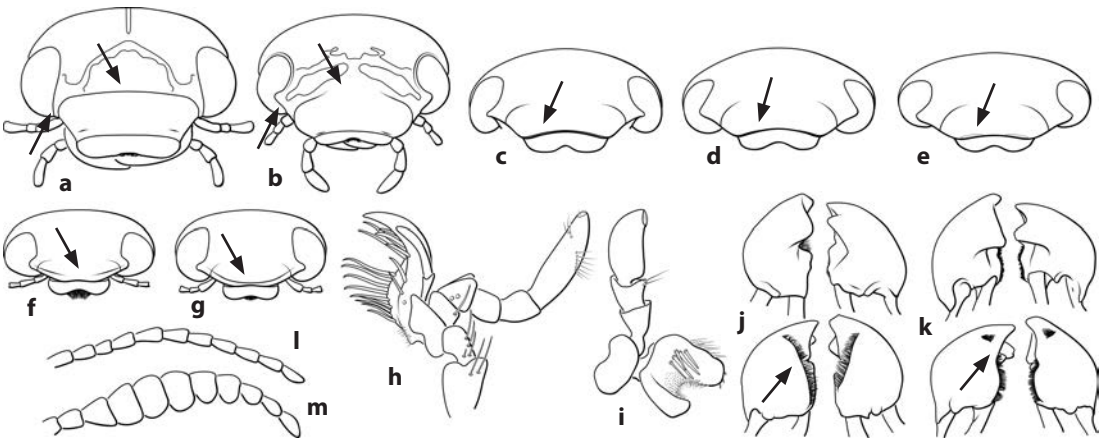


Fig. 2.7. Dytiscidae adult head features. **a**, *Dytiscus marginalis* head. **b**, *Colymbetes exaratus* head. **c**, *Agabus obliteratus* head. **d**, *Ilybiosoma lugens* head. **e**, *Platynectes reticulosus* head. **f**, *Herophydrus inquinatus* head. **g**, *Hygrotus versicolor* mandible. **h**, *Vatellus grandis* maxilla, ventral. **i**, *V. grandis* labium, lateral. **j**, *Dytiscus verticalis* mandibles, ventral left and right (*top*), dorsal right and left (*bottom*). **k**, *Cybister tripunctatus* mandibles, ventral left and right (*top*), dorsal right and left (*bottom*). **l**, *Herophydrus inquinatus* antenna. **m**, *Heroceras descarpentriesi* antenna.

and transversely broad with a distinctive medial gula (Fig. 2.6b). Laterally, there is often a postocular carina extending in a curve from the medial margin of the eye posterolaterally to the margin of the cranium. Many hydroporine taxa — including many members of Hygrotini, Hyphydrini, Pachydrini, and Bidessini — are characterized by the anterior clypeal margin flattened, upturned, anteriorly projecting, or distinctly marginally beaded (Fig. 2.7f,g). An anterior, thin marginal bead may also be present and continuous in *Agabus* (Fig. 2.7c) or discontinuous medially in *Ilybius* and *Ilybiosoma* (Fig. 2.7d). Lateral, elongate foveae are present marginally along the clypeus in many taxa, including Hydrotrupini (Fig. 2.7e).

Mouthparts. Diving beetles have typical adephagan, prognathous, chewing-type mouthparts. The labrum is usually broad and narrowed with a distinctive anterior fringe of dense setae (Fig. 2.7a–g). The mandibles are short and robust, each usually with two apical teeth, a subapical tooth, and a fringe of setae that is interrupted medially in most taxa (Fig. 2.7k) or continuous in Dytiscinae (Fig. 2.7j). The maxilla typically has a small, elongate, lobe-like galea of two segments and a small, elongate, apically pointed and toothed lacinia with medial spines (Fig. 2.7h). The maxillary palpus is elongate and four-segmented (Fig. 2.7h). The labium has a broad, conspicuous mentum that is broadly associated with the cranium, and a smaller medial ligula on which articulates the paired, three-segmented palpi (including the palpiger, Fig. 2.7i). The palpi may be modified in taxon-specific ways. For example, members of *Hydrotrupes* have the palpi short with the

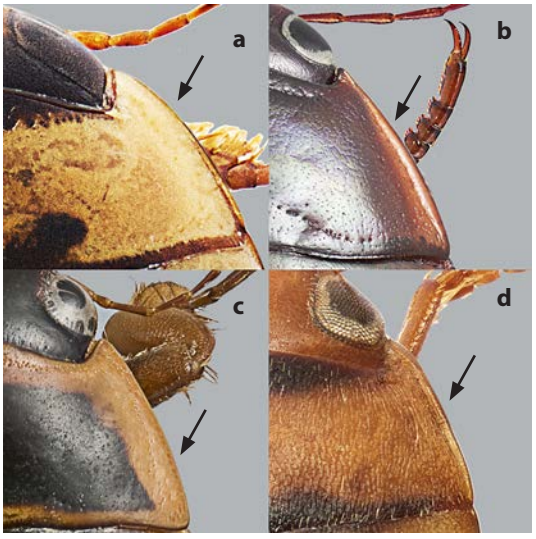


Fig. 2.8. Dytiscidae lateral pronotal surface. **a**, *Coptotomus longulus*. **b**, *Hyderodes shuckardi*. **c**, *Dytiscus marginalis*. **d**, *Neoporus dimidiatus*.

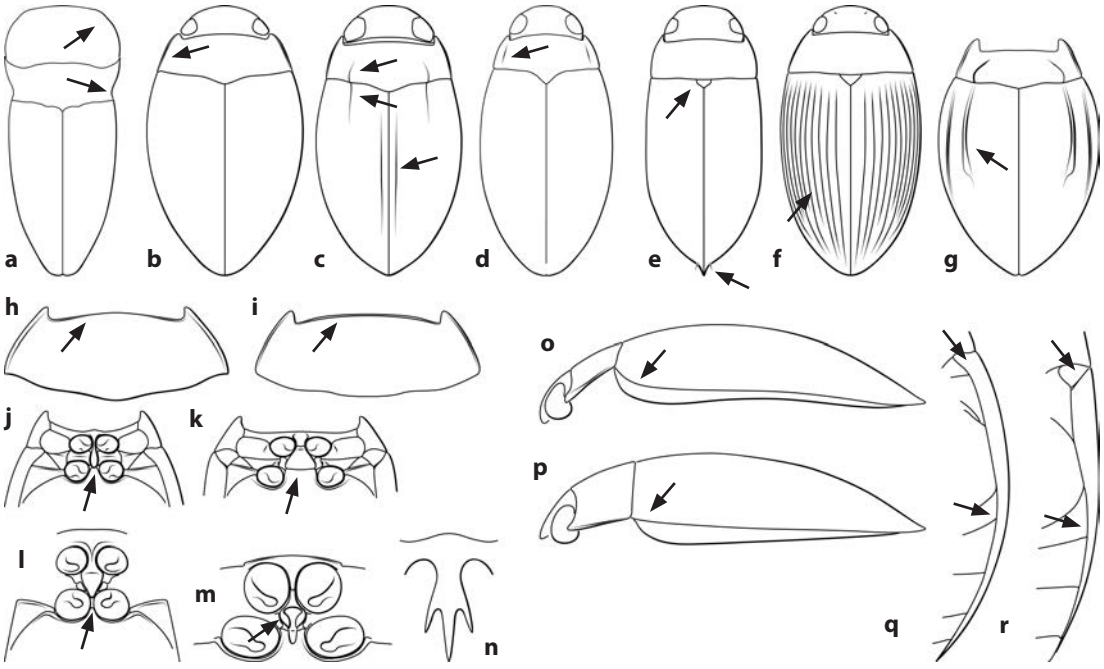


Fig. 2.9. Dytiscidae adult thoracic features. **a**, *Ereboporus naturaconservatus* habitus. **b**, *Hygrotus laccophilinus* habitus. **c**, *Bidessus toumodiensis* habitus. **d**, *Graptodytes bilineatus* habitus. **e**, *Celina hubbelli* habitus. **f**, *Copelatus distinctus* habitus. **g**, *Yola bicarinata* pronotum and elytra. **h**, *Ilybiosoma lugens* pronotum. **i**, *Ilybius ater* pronotum. **j**, *Chostonectes gigas* ventral surfaces. **k**, *Hydrovatus pustulatus* ventral surfaces. **l**, *Tyndallhydrus caraboides* ventral surfaces. **m**, *Desmopachria portmanni* ventral surfaces. **n**, *Neptosternus* sp. prosternal process **o**, *Antiporus gilbertii* lateral aspect. **p**, *Sekaliporus kriegi* lateral aspect. **q**, *Chostonectes gigas* left epipleuron. **r**, *Paroster pallescens* left epipleuron.

apical palpomeres subquadrate (see Fig. 7.3a). Male *Agabus crassipies* (Fall) have the palpi modified into an apparent sound-production structure (Larson and Pritchard 1974). The apical palpomeres may be bifid (as in *Coptotomus*, e.g., Fig. 21.2c). There are usually a pair of apical sensillar patches, though some taxa (e.g., *Pachydrus*) have more than two.

Antennae. Most Dytiscidae have filiform antennae with 11 segments (Fig. 2.7l,m). However, the antennae may range from elongate and slender to short with broad antennomeres. In a very few cases (e.g., *A. antennatus* Leech) the antennae are distinctly clavate. Some groups have the antennae sexually dimorphic and males with modified antennomeres. This is characteristic of many *Sternopriscus* (e.g., Fig. 30.20), *Queda* (e.g., Fig. 33.5), *Hydrovatus*, *Allopachria* (e.g., Fig. 36.12), *Heroceras* (e.g., Figs. 2.7m,35.8), and *Agaporomorphus* (e.g., Fig. 10.9), among others, and is often species specific. They might function as grasping or persistence devices (or other derivatives of sexual selection), but it is also possible they are enlarged areas for chemoreception.

Thorax.

Dorsally, the dytiscid thorax is dominated by the pronotum, scutellum, and elytra. The pronotum is typically broad with variably angulate posterolateral angles and anteriorly produced anterolateral angles (Fig. 2.6a). The lateral margin may be variably curved from nearly straight to strongly curved. In some taxa, particularly rheophilic and subterranean groups, but also others, the pronotum is cordate with the lateral margins strongly curved anteriorly with the entire pronotum widest anterad of the middle (Fig. 2.9a), whereas in most the pronotum is widest at or near the posterior angles (Fig. 2.6a). The lateral margin in most taxa is beaded, with the bead variable among taxa from narrow (Fig. 2.8a) to broad (Fig. 2.8b), or absent in a few taxa such as most Cybistrinae and Dytiscinae (Fig. 2.8c). In a few taxa, like some *Neoporus*, the lateral bead is broader anteriorly and narrowed posteriorly (Fig. 2.8d). Degree of curvature or medial angulation of the posterior margin of the pronotum is variable among taxa and is important for generic diagnostics in Laccophilinae (see Fig. 13.5). The anterior margin may be somewhat beaded or have a submarginal crease or groove that can be continuous, as in *Ilybius* (Fig. 2.9h) or discontinuous medially, as in *Ilybiosoma* (Fig. 2.9i). Members of many Bidessini and a few *Desmopachria* have a short, distinct, incised longitudinal crease or "plica" on each side at the base of the pronotum (Fig. 2.9c). Many Siettitiina and *Oreodytes* have a longitudinal crease medially on each side of the pronotum (Fig. 2.9d).

The scutellum is visible with the elytra closed in many Dytiscidae except nearly all Hydroporinae, Laccophilini, and the dytiscinae genus *Notaticus* (see Fig. 18.3). Among the Hydroporinae, members of *Celina* (Fig. 2.9e) and *Carabhydrus* (see Fig. 30.14) have a distinctly visible scutellum, and

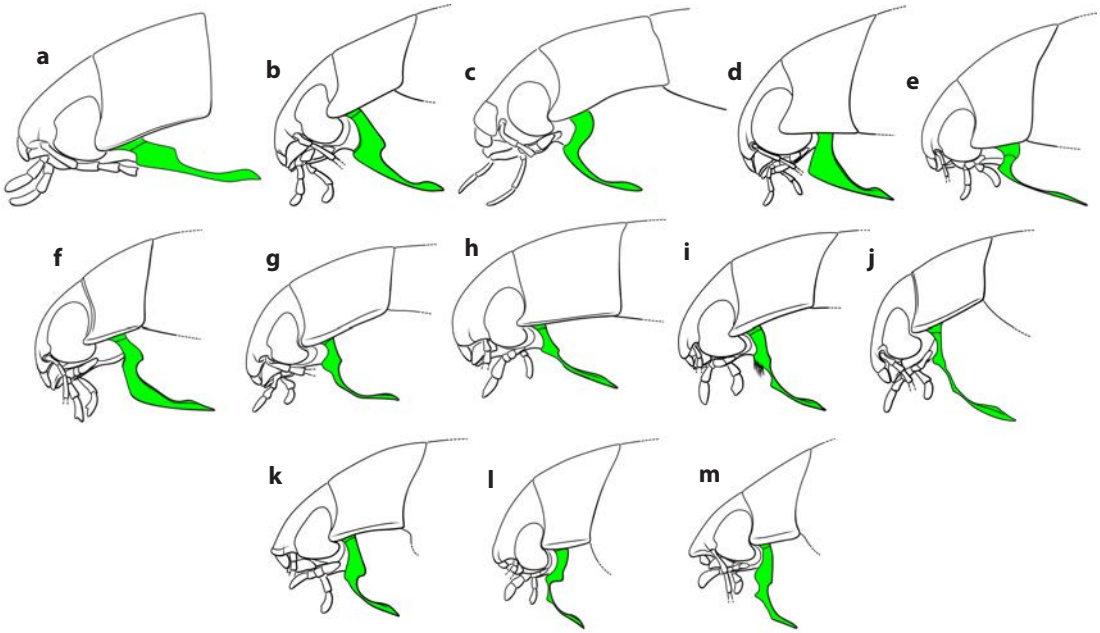


Fig. 2.10. Dytiscidae lateral aspect showing prosternal process. **a**, *Copelatus distinctus*. **b**, *Colymbetes fuscus*. **c**, *Dytiscus marginalis*. **d**, *Cybister tripunctatus*. **e**, *Laccophilus maculosus*. **f**, *Coptotomus longulus*. **g**, *Celina* sp. **h**, *Lioporeus triangularis*. **i**, *Heterosternuta wickhami*. **j**, *Coelambus impressopunctatus*. **k**, *Allopachria quadripustulata*. **l**, *Microdytes sabitae*. **m**, *Pachydrus* sp.

members of *Hydrocolus* have at least apical portions of the scutellum visible (see Fig. 27.10).

The prosternum is usually short and broad (Fig. 2.6b). Laterally, where the prosternum meets the pronotal epipleuron, there is often a small emargination, but in some Hydroporinae there is a small pore at this suture. The shape of the middle of the prosternum is often variable with some taxa having this area evenly rounded, others medially carinate or tectiform, and others with setae or other shape modifications. The prosternal process extends from the medial portion of the prosternum posteriorly between the procoxae where it is distinctly constricted. In many Hydroporinae, there is a distinctive tubercle or transverse ridge medially between the procoxae. The shape and nature of the prosternal process are very important for diving beetle diagnostics and exceptionally variable across the group. In some it is medially carinate, others nearly flat. In some, it is apically acuminate or narrowly pointed (Fig. 2.9j), in others apically broadly truncate (Fig. 2.9k). In most diving beetles, the prosternal process extends between the mesocoxae to the metaventrite (Fig. 2.9j,k), but in others, especially rheophilic and subterranean groups but also members of Vatellini, the prosternum does not extend to the metaventrite and the mesocoxae are contiguous (Fig. 2.9l). An important historical character is the degree of dorsoventral curvature of the prosternal process. Members of Hydroporinae (and Coptotominae) have the prosternal process in a distinctly different, more ventral plane than the anterior portion of the prosternum (Fig. 2.10f–m). Other Dytiscidae have the prosternal process and anterior portion of the prosternum in the same plane, which may be at the same level as the posterior portion of the cranium (Fig. 2.10a–c,e), or may be entirely lower (more ventral) than the posterior portion of the cranium (Fig. 2.10d). Members of *Neptosternus* have the prosternal process conspicuously trifid (Fig. 2.9n), and a few members of *Desmopachria* have males with the process bifurcated with a deep pit between the branches (Fig. 2.9m).

The mesoventrite is small and forms a fork that contains the prosternal process that largely obscures it in ventral aspect. Other thoracic sclerites — including the propleuron, mesepimeron, mesepisternum, and metathoracic anepisternum — are usually relatively undifferentiated among taxa. Together, the propleuron, mespimeron, and anterior surface of the metathoracic anepisternum form a deep concavity in the anterior portion of the beetle for reception of the pro- and mesothoracic legs.

The metaventrite (metasternum of many previous authors) is large and transverse. Anteriorly in most taxa it extends in a short process between the mesocoxae to interface with the prosternal process (Fig. 2.6b). Laterally the metaventrite extends nearly to the elytral epipleuron, separated from it by a suture between the metacoxa and the metathoracic anepisternum (Fig. 2.6b). The lateral extensions of the metaventrite are often call the "metasternal wings" and are variable in their degree of curvature and width (Fig. 2.6b). The metaventrite has a distinctive longitudinal, medial suture ("median metasternal suture" or "discrimen") (Fig. 2.6b), but there is no transverse suture on the metaventrite (Fig. 2.6b).

Elytra. Diving beetle elytra are usually relatively simple, smooth, and streamlined. They typically conform closely to the shape of the abdomen, covering all the tergites or with the apical tergite extending posteriorly beyond the apex of the elytra. The elytra form a shell that holds air above the tergites where the spiracles can be exposed to the air. The apex of the elytron may have a variety of shapes, including spines or truncations.

Numerous groups are characterized by longitudinal grooves on the elytral disc — e.g., *Copelatus* (Fig. 2.9f), some *Dytiscus* (see Fig. 16.6b,d) and *Acilius* females (see Fig. 20.11b), *Barretthydrus* (see Fig. 30.12), etc.) — complex irregularities — e.g., some *Hyderodes* (see Fig. 16.7c) and *Graphoderus* (see Fig. 20.13c) females — or longitudinal carinae or costae — e.g., *Yola* (Fig. 2.9g). It appears likely that only in *Copelatus* are the grooves homologous with the discal series of punctures present in most Dytiscidae. The grooves in other taxa are *de novo* character states, some of which (e.g., *Acilius* and *Dytiscus*) are present in females and are associated with their sexual strategy (see Chapter 1). Species are often characterized by short, longitudinal striae or "plicae" at the base, especially many Bidessini (Fig. 2.9c). A particularly important character system at the species level in many groups is the nature of the punctation and surface sculpturing (incised lines) (Wolfe and Zimmerman, 1984). Punctures may have characteristic shapes, densities, or sizes or may be absent altogether. Many species that are otherwise smooth have a basic generalized pattern of four series of punctures, a subsutural series and three additional discal series. Sculpture may include short, inscribed lines or widespread anastamozing lines forming a network of meshes, sometimes with primary meshes with additional secondary meshes between the main lines.

The ventral surface of the elytra has a number of features that have been used in phylogenetic reconstruction and classification of diving beetles including the presence of a variable apicoventral patch

of setae in many Dytiscinae and Cybistrinae (Miller, 2001c). Also, elongate, irregular carinae and lobes laterally on the ventral surface are variable, particularly among Hydroporinae, and especially Hyphydrini (Wolfe, 1985; 1988; Biström *et al.*, 1997b).

The elytral epipleuron in diving beetles is distinctly delimited from the dorsal surface of the elytron by a lateral carina which extends from the humeral angle posteriorly to nearly the apex of the elytron. The relative curvature of the epipleural carina in lateral aspect varies among taxa, and can be an important diagnostic character for certain genera, such as some Sternopriscina (Fig. 2.9o,p), and among certain species, such as in *Hydroporus*. In most diving beetles, the epipleuron is broader anteriorly and abruptly constricted medially and narrower in the apical half (Fig. 2.9r). Some groups, such as many Sternopriscina and *Deronectes* (Fig. 2.9q),

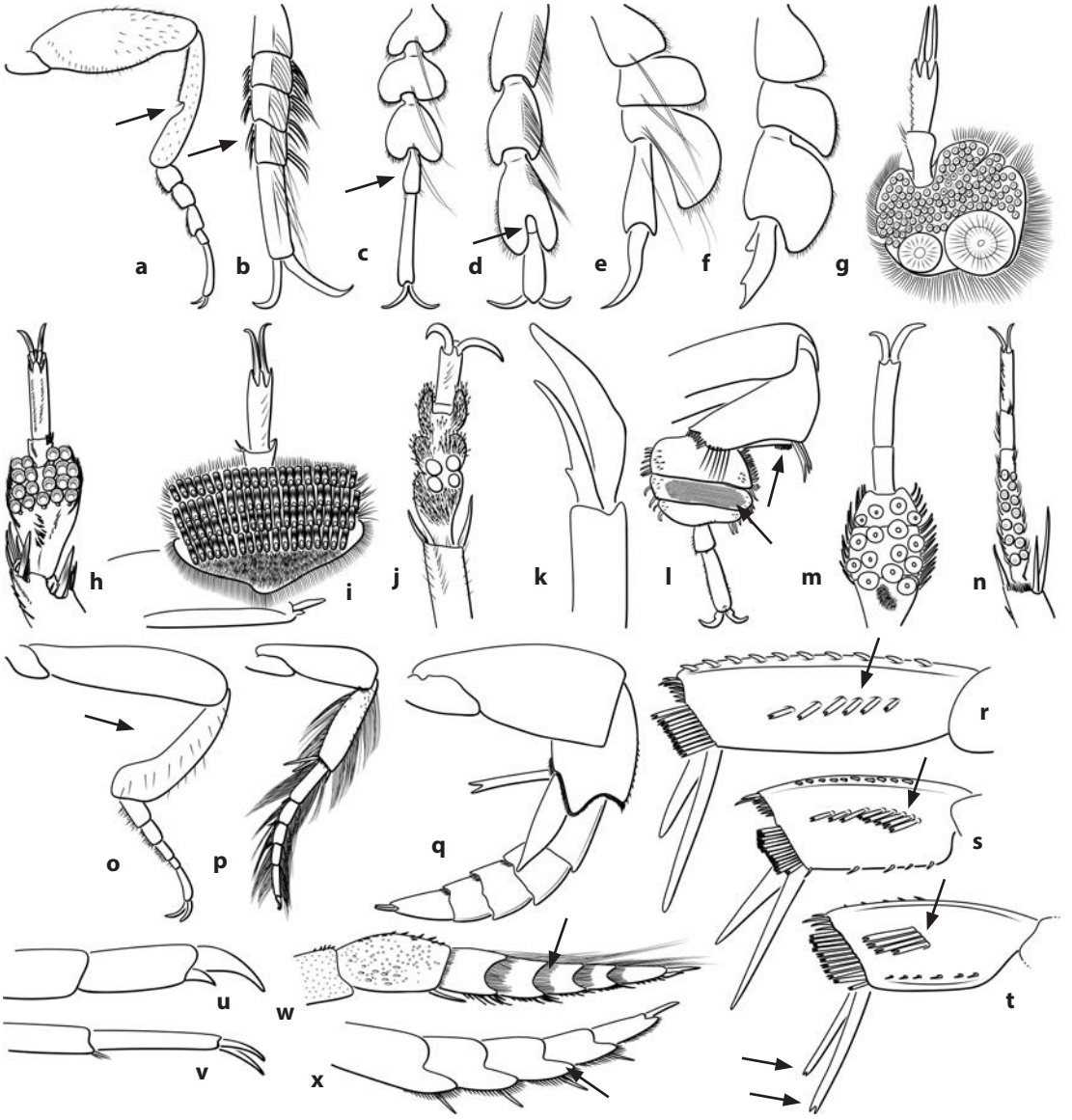


Fig. 2.11. Dytiscidae adult legs. **a**, *Necterosoma penicillatum* male proleg. **b**, *Rhantus atricolor* protarsi. **c**, *Necterosoma penicillatum* protarsus. **d**, *Chostonectes gigas* protarsus. **e**, *Sekaliporus kriegi* protarsus. **f**, *Tiporus josepheni* protarsus. **g**, *Dytiscus marginalis* male protarsus, ventral aspect. **h**, *Colymbetes fuscus* male protarsus, ventral aspect. **i**, *Cybister sp* male protarsus, ventral aspect. **j**, *Oreodytes quadrimaculatus* male protarsus, ventral aspect. **k**, *Agabus bipustulatus* protarsal claws. **l**, *Hydaticus aruspex*, male proleg. **m**, *H. aruspex* male mesotarsus, ventral aspect. **n**, *Aethionectes fulvonotatus* male mesotarsus, ventral aspect. **o**, *Bidessonotus tibialis* male mesoleg. **p**, *Agabus obsoletus* male metaleg. **q**, *Megadytes lherminieri* metaleg. **r**, *Hydaticus aruspex* metatibia, posterior aspect. **s**, *H. flavolineatus* metatibia, posterior aspect. **t**, *Acilius abbreviatus* metatibia, posterior aspect. **u**, *Pachydrus* sp. metatarsal claws. **v**, *Coelambus patruelis* metatarsal claws. **w**, *Acilius sinensis* metaleg. **x**, *Laccophilus proximus*, metatarsus.

have the epipleuron broad throughout the length of the epipleuron without the distinctive medial constriction. A number of unrelated taxa have the posterior, humeral region of the epipleuron delimited from the posterior portion by a prominent, oblique, transverse carina (Fig. 2.9r). In many of these taxa, the anterior, humeral region is distinctly concave and receives the apex of the mesofemur.

Flight wings. There are only a few known diagnostic features associated with the dytiscid metathoracic wings. Dytiscids have the typically reduced variation associated with Adephaga and include a well-developed oblongum cell and conspicuous subcubital binding patch (Sharp, 1882; J. Balfour-Browne, 1940; Hammond, 1979). A number of species are or appear to be wingless (and therefore flightless), especially, but not exclusively, hyporheic or subterranean species (Franciscolo, 1983; Smrž, 1983; Larson and Labonte, 1994; Spangler, 1996; Watts and Humphreys, 1999). Other species are dimorphic, with some specimens winged and others wingless (Leech, 1942; Jackson, 1956b).

Prolegs. The prothoracic legs are used for grasping prey items or the substrate and other sorts of activities and are usually retracted during swimming, though the femur, tibia, and tarsomeres often do have swimming hairs. The procoxa is movable. The prolegs are also often used by males to grasp females for mating, and, of the three pairs of legs, exhibit the greatest number of sexually dimorphic modifications. The protrochanter is variously modified in males of some species, including some *Hyphydrus*. The profemur of males of a few taxa, including some *Hygrotus,* may be modified and sculptured. The protibia may be more strongly curved in males or may have distinct imarginations that may be used to grasp females, such as in *Necterosoma* (Fig. 2.11a) and *Sternopriscus*, among others. The protarsi are distinctly pentamerous in many diving beetle groups, though the fourth tarsomere may be relatively small (Fig. 2.11b). Tarsomere V is usually the longest (Fig. 2.11b). Most Hydroporinae, however, are pseudotetramerous with tarsomere IV small and concealed between the lobes of tarsomere III (Fig. 2.11d) except in certain genera such as *Sternopriscus*, *Necterosoma*, and *Bidessonotus,* which are more distinctly pentamerous (Fig. 2.11c). In a few taxa, such as males of certain members of Sternopriscina, the protarsi are actually tetra- or trimerous (Fig. 2.11e,f). Tarsomeres I–III in Hydroporinae are typically broader, and often ventrally lobed (Fig. 2.11c–f). The protarsomeres exhibit considerable sexual dimorphism. In most diving beetles, male protarsomeres I–III are more broadly expanded and often have large fields of ventral adhesive setae (e.g., Fig. 2.11g–j). This reaches particular exaggeration in members of Dytiscinae that have protarsomeres I–III together broadly expanded, rounded, and ventrally bearing conspicuous, sucker-shaped adhesive discs (Fig. 2.11g). These modifications are used to grasp females prior to and during the mating event. Often the degree and type of expansion are species specific. In a few groups, mainly in Hydroporinae, there is no variation between males and females, but often one of the best or only ways to confirm the sex of a specimen is a comparison of protarsomere expansion. Finally, the protarsal claws are often sexually dimorphic in a species-specific way with male claws asymmetrical, more strongly curved, elongate, or toothed (e.g., Fig. 2.11k). A few additional, unusual modifications exist in certain groups, including dense pencils of setae on the male protrochanter, or the stridulatory device formed by a field of pits on the dorsal surface of protarsomere II and a series of pegs on the protibia in most *Hydaticus* (Fig. 2.11l), and other modifications.

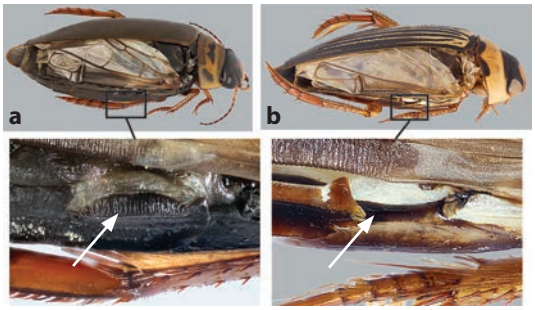


Fig. 2.12. Dytiscidae abdominal pleurite II. **a**, *Colymbetes exaratus*. **b**, *Lancetes lanceolatus.*

Mesolegs. The mesothoracic legs, like the prolegs, are used primarily for grasping the sub-

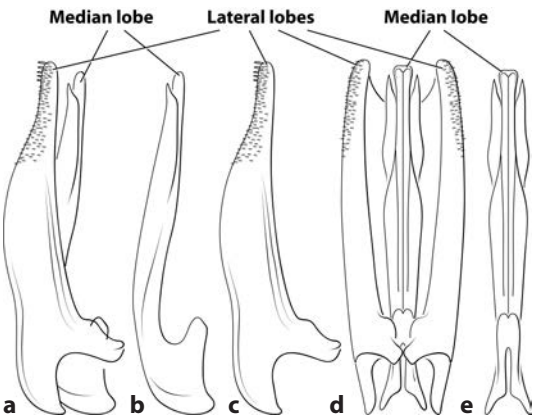


Fig. 2.13. *Eretes sticticus* male aedeagus. **a**, Median and right lateral lobe, right lateral aspect. **b**, Median lobe, right lateral aspect. **c**, Right lateral lobe, right lateral aspect. **d**, Median and lateral lobes, dorsal aspect. **e**, Median lobe, dorsal aspect.

strate, prey items, or mates (by males) and for steering while swimming. They are similar to the prothoracic legs in having a movable coxa and similarly shaped structures, and the tarsi may be (like the protarsomeres) pseudotetramerous, as in most Hydroporinae, or more distinctly pentamerous, as in other diving beetle subfamilies. Mesotarsal claws and/or mesotarsi are modified in males of some species, such as some *Agaporomorphus*, for grasping mates. Claws may be variously curved, and often mesotarsomeres have ventral adhesive setae of various types (Fig. 2.11m,n), similar to the prolegs, though often to a lesser degree. The mesofemur is more strongly curved in some taxa such as *Bidessonotus* (Fig. 2.11o).

Metalegs. The metathoracic legs are the primary legs used for thrusting the beetle through the water during swimming and exhibit a number of modifications related to this. The metacoxae are dramatically enlarged and anteriorly expanded, forming the origin of large coxal-trochanteral muscles that drive the rearward thrust of the leg (Fig. 2.11p,q). Like other Adephaga, the metacoxa is fused to the body wall, and the entire leg is rotated 90º such that the anatomically anterior surface of the leg is directed ventrally (Miller and Nilsson, 2003), an orientation that maximizes forward thrust (Bell, 1967). The metafemur and especially the metatibia and metatarsomeres are often broadly expanded (Fig. 2.11q), thereby increasing the surface area used to push against the water, though they may be long and slender in some taxa (Fig. 2.11p). Long fringes of natatory, or swimming, setae are present along the dorsal and/or ventral margins of the metatibia and metatarsomeres, which can be expanded to provide greater surface area to thrust against the water. These hairs can be collapsed against the leg, and the broad metatibia and metatarsomeres can be turned on their sides and brought near the body during the forward stroke. The metatarsal claws vary in relative size among diving beetle taxa with some species having two claws subequal in length (Fig. 2.11v), others with one claw shorter than the other (Fig. 2.11u, either anterior or posterior claw shorter), and some taxa with only a single claw. A few species (e.g., females of some *Cybister*) are polymorphic with some individuals having a single claw and others having a short second claw.

The apex of the metatibia has a pair of spurs that may be apically bifid, as in Aciliini (Fig. 2.11t) and *Laccophilus*, or simple. Members of Cybistrinae have the anterior spur broader than the posterior and apically acuminate (Fig. 2.11q). Other spines on the metalegs are also diagnostic. Members of Hydaticini, Eretini, and Aciliini have series of very short setae along the anterior margins of the metatarsomeres (and mesotarsomeres) (Fig. 2.11w). The dorsal surface of the metatibia has a series of setae that may be apically bifid and in a linear (Fig. 2.11r), curved (Fig. 2.11s), oblique (Fig. 2.11t), or clustered series.

The metatarsomeres are often distinctly lobed apically, particularly in Laccophilini, which have prominent anteroventral lobes (Fig. 2.11x), though other taxa also may be lobed.

Abdomen.

The dytiscid abdomen has six visible ventrites that are the manifestations of actual sternites II–VII (sternite I reduced and not externally visible). As with other Adephaga, the first visible abdominal ventrite (II) is medially divided by the metacoxae (Fig. 2.6b). In some taxa (Bidessini, Pachydrini, some Hyphydrini), ventrite II is fused with the metacoxae. Sternites III–IV are nearly fused in many taxa with the suture most distinctly visible only laterally (Fig. 2.6b). There are an additional three ventrites (sternites V–VII) then visible (Fig. 2.6b). Sternite VIII is medially longitudinally divided and invaginated into the abdomen, where it is incorporated somewhat into the external genitalia. The main modifications to the abdominal sternites are to visible sternite VI (the last visible sternite), which may be variously rugulose, emarginate, spined, asymmetrical, or modified in other ways, particularly in males (e.g., Fig. 2.14a). A few additional taxa have medial spines or other structures in the male (e.g., some *Hyphydrus* and *Agaporomorphus*), and some have a stridulatory device with ridges on the abdominal sternites that interface with the metafemur or tibia (e.g., in some *Agabus*).

Abdominal tergites and pleural regions have been little studied for variation among taxa, but in Colymbetini and a few Dytiscinae (*Dytiscus* and *Hyderodes*) the surface of pleurite II (oriented dorsally and concealed under the lateral margin of the elytron) is conspicuously transversely rugose (Fig. 2.12a), but in others it is not (Fig. 2.12b).

Members of *Hydrovatus* and Methlini have the apex of the abdomen modified in a complex way (Wolfe, 1985; 1988). The abdominal tergites and sternites are subdivided into additional sclerites and, together with the terminal sternite, form an acuminate apex (Fig. 2.14c) of unknown function though they may be used to access plant vacuoles for breathing (Wolfe, 1985; 1988).

Male genitalia. The male genitalia consist

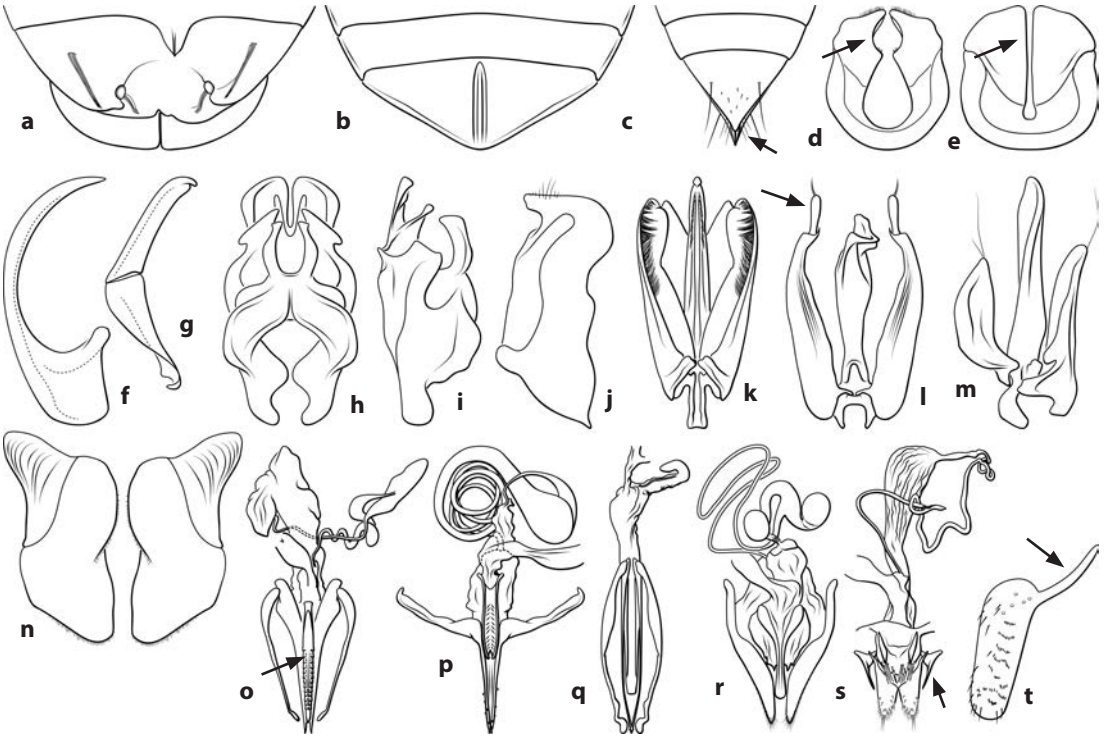


Fig. 2.14. Dytiscidae adult abdominal features. **a**, *Africophilus nesiotes* male terminal abdominal ventrites. **b**, *Agabetes acuductus* male terminal abdominal ventrites. **c**, *Methles cribratellus* male terminal abdominal ventrites. **d**, *Cybister tripunctatus* male sternite VIII. **e**, *Megadytes fraternus* male sternite VIII. **f**, *Liodessus affinis* male median lobe, right lateral aspect. **g**, *L. affinis* right lateral lobe, right lateral aspect. **h**, *Desmopachria volatidisca* male median lobe, dorsal aspect. **i**, *D. volatidisca male* median lobe, right lateral aspect. **j**, *D. volatidisca* male lateral right lateral lobe, right lateral aspect. **k**, *Dytiscus thianshanicus* aedeagus, dorsal aspect. **l**, *Copelatus* sp aedeagus, dorsal aspect. **m**, *Laccophilus maculosus* aedeagus, dorsal aspect. **n**, *Megadytes glaucus* gonocoxosternites. **o**, *Laccomimus* sp. female reproductive structures, ventral aspect. **p**, *Hydrovatus pustulatus* female reproductive structures, ventral aspect. **q**, *Hydaticus aruspex* female reproductive structures, ventral aspect. **r**, *Nebrioporus dubius* female reproductive structures, ventral aspect. **s**, *Laccornis oblongus* female reproductive structures, ventral aspect. **t**, *Hydrodytes inaciculatus* left gonocoxa.

in a larger series of structures called the genital capsule, which includes sternites VIII and IX, pleurites IX, tergite IX, and the aedeagus, though homology of many of these structures is somewhat ambiguous. Sternite VIII is longitudinally deeply and nearly entirely subdivided, and in *Cybister* has the medial margin emarginate (Fig. 2.14d), whereas in other taxa it is entire (e.g., Fig. 2.14e). The other tergites, pleurites and sternites form a ring-shaped structure with muscle attachments within which the aedeagus occurs at repose. Other than the aedeagus, which is used extensively in dytiscid diagnostics, however, these male structures have not been much examined for useful characters though they are variable across taxa.

The primary known diagnostic portions of diving beetle male genitalia are associated with the aedeagus, which is composed of an elongate median lobe with a pair of lateral lobes, each of which articulates at its base with the lateral base of the median lobe (Figs. 2.13d,14k–m). Often, authors refer to the lateral lobes as parameres, and then may refer to only the median lobe as the aedeagus. Terminology for these structures has not been entirely stabilized. The entire aedeagus is usually rotated about 90º when at rest inside the end of the abdomen, and rotates to 180º from its anatomical position when extended, though it is then curved anterad under the male to insert into the female (Sharp and Muir, 1912; Miller and Nilsson, 2003). Evidence for this rotation or "retournement" (Jeannel, 1955) comes from the orientation of the trachea, which twists around the genital capsule as the result of this rotation (Sharp and Muir, 1912). Miller and Nilsson (2003) advocated for referring to the original anatomical orientation of the aedeagus when describing structures and surfaces of the aedeagus, a convention that has not always been used consistently.

The median lobe exhibits extensive diversity across the group, varying in shape from a relatively simple, elongate, curved structure (e.g., Fig. 2.14f) to a complex apparatus with flanges, setae, spines, and highly varied features (e.g., Fig. 2.14h,i). The basic structure (Fig. 2.13) is a relatively robust

basal portion with an elongate, dorsally curved apical portion with a ventral groove that bears a membranous tube ending in a subapical gonopore. Diving beetles do not have a well-developed internal sac, or endophallus. In Dytiscinae the ventral groove is large and expanded and bears an elongate ventral sclerite that expands, allowing the passage of the spermatophore. In Dytiscinae (Fig. 2.14k) and most Hydroporinae (plesiomorphically in both groups, but reversed multiple times in Hydroporinae) the median lobe is bilaterally symmetrical. In most other diving beetles the median lobe is somewhat to distinctly asymmetrical and variously twisted (Fig. 2.14l,m).

The lateral lobes articulate independently near the base of the median lobe (Fig. 2.13). They are often not as strongly variable across a group compared with the median lobe but do regularly bear important diagnostic features, and, in some cases, are dramatically modified and may be as, or more, prominent than the median lobe, as in many *Desmopachria*, for example (Fig. 2.14j). In Laccophilini the lateral lobes are asymmetrical (Fig. 2.14m), but in most other diving beetles the lateral lobes are symmetrical (Fig. 2.14k,l), even in those groups with bilaterally asymmetrical median lobes (Fig. 2.14l). The lateral lobes often have apical setal brushes or fringes of setae along the dorsal margins. Most members of Bidessini have the lateral lobes distinctly bi- or trisegmented (e.g., Fig. 2.14g), and many Copelatinae have a distinct apical lobe with a characteristic apical pencil of setae (Fig. 2.14l).

Female genitalia. Dytiscid external female genitalia (the ovipositor) exhibit considerable variability across the diversity of the group, much of which is taxon specific. This is not surprising given the considerable range of variation in oviposition techniques. The structures include paired gonocoxosternites that may be homologous with sternite VIII, but, if so, the structure is longitudinally entirely divided into two large sclerites (Fig. 2.14n). Additional structures associated with the ovipositor are paired, single-segmented gonocoxae, each of which articulate anteriorly with a laterotergite that extends posteriorly alongside the gonocoxae when at rest (Fig. 2.15). The laterotergites articulate posteriorly such that these structures are folded at rest and are levered outward for oviposition (Fig. 2.15). Medially, between the gonocoxae, there may be variably sclerotized, paired, elongate structures called rami subtending the gonopore (Fig. 2.15). Each of these sclerites is variable depending on the taxon and probably based on type of oviposition, whether endophytically, into deep cracks, among vegetation, etc.

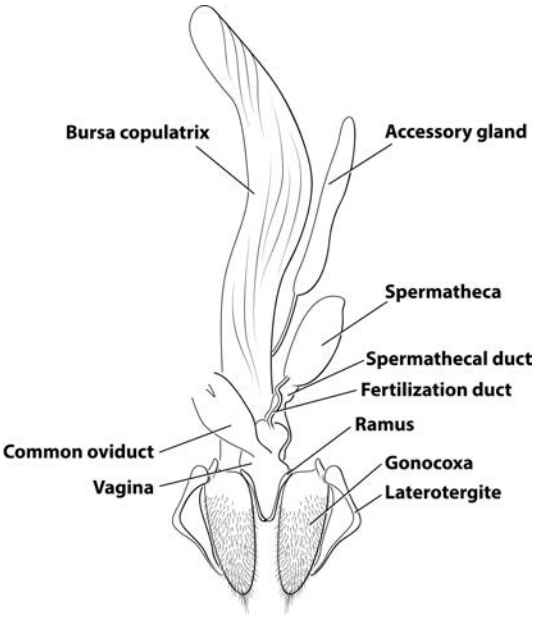


Fig. 2.15. *Rhantus binotatus* female external and internal reproductive structures, ventral aspect.

Several taxa oviposit endophytically, including Cybistrinae, Laccophilinae, *Hydrovatus* many Dytiscinae, and some Agabinae. These specimens often have the gonocoxae fused and together knife-like and sometimes serrated (Fig. 2.14o–q). Members of certain Agabinae and Laccophilinae, in particular, have the rami serrated (Fig. 2.14o). *Hydrovatus* have the anterior portion of the gonocoxae extending laterally (Fig. 2.14p). Major variation in the external genitalia also includes loss of the laterotergite in all Hydroporinae (Fig. 2.14r) except Laccornini (Fig. 2.14s, and possibly Pachydrini, Burmeister, 1976; Miller, 2001c). The gonocoxae may be elongate and slender, as in many Copelatinae and Dytiscinae (Fig. 2.14q), or short, flattened, and broad, as in many Colymbetini (Fig. 2.15). The gonocoxae are often covered with numerous fine setae, and most diving beetles have a variable, apical pencil of setae (Fig. 2.15). Members of Hydrodytinae and Hydroporinae have the gonocoxae with an elongate, anterior apodeme, or extension (Fig. 2.14t).

The diving beetle internal female genitalia (reproductive tract, or RT) is unusual among arthropods in its organization into a "loop" with two genital openings (Fig. 2.15; Heberdey, 1931; Jackson, 1960b; Burmeister, 1976; Miller, 2001c). One opening is to the bursa copulatrix ("bursa") (Fig. 2.15), which receives the sperm (or spermatophore) from the male. The bursa often has an associated gland (Fig. 2.15), though this is absent in many taxa, including Hydroporinae (Fig. 2.14r,s). A spermathecal duct leads from the bursa to the spermatheca (Fig.

2.15). In many taxa, the duct is extremely elongate and slender (Fig. 2.14p,r) or may exhibit other complex variation, including internal setae, small glands, etc. (Figs. 2.14o–s,15). The spermatheca is often convoluted, multichambered, or otherwise modified (Fig. 2.14r). A fertilization duct leads from the spermatheca to the vagina near the base of the common oviduct (Fig. 2.15). The fertilization duct may also be extremely long and slender, shorter, or otherwise modified (Fig. 2.15). The common oviduct opens into the vagina near the insertion of the fertilization duct, and the vagina opens at the apex of the abdomen for oviposition of eggs. Dytiscids have very dramatic variation in RT morphology across the Dytiscidae, with the greatest diversity (and complexity) within Hydroporinae and Copelatinae, characterized by extra chambers, exceptionally long ducts, setae, large spines, sculpturing, and other dramatic modifications. Members of Dytiscinae, in contrast, have a reduced RT. They have, secondarily, one genital opening and overall lower diversity and complexity (Fig. 2.14q).

Miller (2001c) characterized four configurations of female RT in Dytiscidae. One is the "Amphizoid type" with two genital openings and the spermathecal duct extending from the posterior base of the bursa. In diving beetles, this configuration is characteristic of Matinae and many Colymbetinae (Fig. 2.15) and Agabinae. Another RT configuration is the "Hydroporine type" with the spermathecal duct attached at the anterior apex of the bursa (Fig. 2.14p,r,s). This configuration is typical of Hydroporinae, Lancetinae, Copelatinae, Coptotominae, Laccophilinae, and some Colymbetinae and Agabinae. A third type, the "Dytiscine type," has a single genital opening with both the fertilization duct and spermathecal duct extending from the vagina/bursa to the spermatheca (Fig. 2.14q). This condition is secondarily derived in Cybistrinae and Dytiscinae (Miller, 2001c) and is similar to the condition found in Noteridae and Gyrinidae. In these taxa, the spermatophore is transferred to a separate area ventral to the main female RT (Aiken, 1992). The fourth RT type is the "*Agaporomorphus* type" wherein the bursa appears to be completely reduced, which occurs only in the copelatine genus *Agaporomorphus*.

Internal structures.

A few adult internal structures have been investigated for diagnostic features, including the metafurca (Ríha, 1955; F. Balfour-Browne, 1961) and the proventriculus (F. Balfour-Browne, 1934a; 1935b; 1944; Smrž, 1982), each of which exhibit character variation at several taxonomic levels. The metafurca was used, in part, to determine the subfamilial status of Hydrodytinae by Miller (2001c), and the proventriculus was used to place *Peschetius* with Bidessini by Miller *et al.* (2006). Other internal features have not been comprehensively surveyed across the group.

Sexual dimorphism.

Distinguishing between males and females of Dytiscidae is not usually problematic. Size may be biased toward either larger males or larger females, depending on the species (Zimmerman, 1970; Aiken and Wilkinson, 1985; Ribera, 1994; Fairn *et al.*, 2007). More useful for distinguishing species are the typically more broadly expanded protarsomeres I–III in males, which usually also have a field of ventral adhesive setae (Fig. 2.11h–j). Adhesive setae are missing in a few taxa, but males nearly always have broader protarsomeres than females. Males often also have additional modifications, including: (1) broader or modified antennomeres (e.g., Fig. 2.7m); (2) more strongly curved, longer, broader, or otherwise modified pro- or mesotarsal claws (Fig. 2.11k); (3) modifications to other portions of the legs (Fig. 2.11a,o); (4) stridulatory devices on portions of the legs or abdomen (e.g., Fig. 2.11l); and (5) modifications to the abdominal sterna, including spines, rugae, emarginations, or other features, particularly on sternite VI (for a review, see Miller and Bergsten, 2014b). A few taxa have dimorphic prosternal processes, such as some *Desmopachria,* which have the male process bifid and medially deeply emarginate (Fig. 2.9m).

Males and females often differ in the surface sculpturing on the cuticle, especially on the dorsal surface. The sculpturing may be present on the female and absent on the male, or different in its form or extent. Usually, the female is more strongly sculptured, though females of many species are also dimorphic. In some cases the difference in sculpturing has been suggested to derive from a sexual conflict strategy wherein females attempt to interfere with male tarsal adhesion to the cuticle surface (Miller, 2003; Bergsten and Miller, 2007; Karlsson Green *et al.*, 2013; Miller and Bergsten, 2014a).

3. Keys to Major Groups of Dytiscidae

Key to Adults of the Subfamilies

Although the subfamilies of diving beetles used here are monophyletic as currently defined (Miller and Bergsten, 2014a), distinct morphological features for use in a clean, linear dichotomous key to subfamilies are difficult to find. Many of the most important features for grouping dytiscids into subfamilies are subtle or require dissection or special knowledge. Therefore this key is somewhat artificial, and some subfamilies key out in multiple places as a compromise to make the key easier to use.

1 Eyes absent or strongly reduced (Fig. 3.1a); cuticle depigmented; elytra often fused and metathoracic wings absent or reduced; natatory setae often absent; subterranean or terrestrial . . . . . see key to subterranean taxa below

1' Eyes present, not reduced (Fig. 3.1b); cuticle pigmented; elytra rarely fused, metathoracic wings usually present (reduced or absent in some species); natatory setae usually present; epigean. 2

2(1) Scutellum not visible with elytra closed (Fig. 3.2a,b), or nearly completely obscured (Fig. 3.2c). 3

2' Scutellum clearly visible with elytra closed (Fig. 3.2d) 5

3(2) Prosternum distinctly declivitous with prosternal process in a distinctly different plane from medial portion of prosternum (Fig. 3.3a, also see Fig. 2.10g–m); protarsi pseudotetramerous with a small tarsomere IV concealed within paired ventral lobes of tarsomere III (Fig. 3.4a), a few isolated hydroporine taxa, *Bidessonotus*, *Necterosoma,* and *Sternopriscus*, with protarsi more evidently pentamerous (Fig. 3.4b), but these taxa with prosternal process distinctly declivitous) . . . . . Hydroporinae (in part), 138

3' Prosternum not strongly declivitous, prosternal process in same plane as medial portion of prosternum (Fig. 3.3b, also see Fig. 2.10a–f, though in some cases anterior margin of prosternum may be different plane from ventral surface of head (e.g., Fig. 2.10d,f)); protarsi distinctly pentamerous, tarsomere IV distinct and tarsomere III not ventrally bilobed (Fig. 3.4c). 4

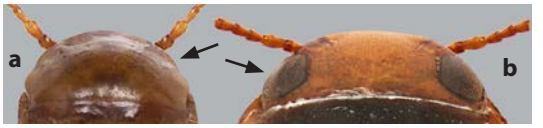


Fig. 3.1. Hydroporinae heads. **a**, *Kuschelydrus phreaticus*. **b**, *Heterosternuta pulchra.*

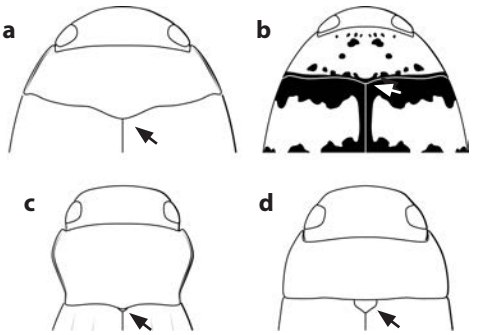


Fig. 3.2. Dytiscidae dorsal surfaces. **a**, *Sanfilippodytes* sp. **b**, *Notaticus fasciatus*. **c**, *Carabhydrus niger*. **d**, *Celina hubbelli.*

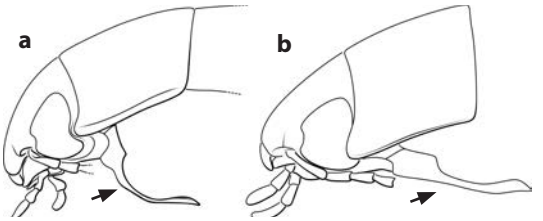


Fig. 3.3. Dytiscidae prosternal processes. **a**, *Celina hubbelli.* **b**, *Copelatus distinctus.*

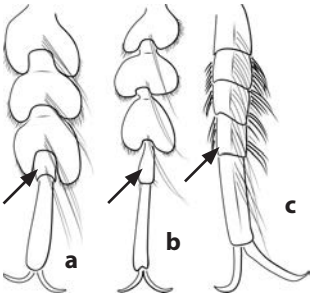


Fig. 3.4. Dytiscidae protarsi. **a**, *Barretthydrus tibialis*. **b**, *Necterosoma penicillatum*. **c**, *Rhantus atricolor*.

4(3) Metatarsus with a single claw (Fig. 3.5a); metatarsomeres I–IV conspicuously lobed at posteroapical margin (Fig. 3.5a) . . . . . Laccophilinae (in part), Laccophilini, 91

4' Metatarsus with two claws (Fig. 3.5b); metatarsomeres I–IV not conspicuously lobed at posteroapical margin (Fig. 3.5b) . . . . . Dytiscinae (in part), Aubehydrini, 121

5(2) Protarsi pseudotetramerous in both sexes, tarsomere IV small and concealed within lobes of III (as in Fig. 3.4a). . .Hydroporinae (in part) 6

5' Protarsi distinctly pentamerous in both sexes (Fig. 3.4c) but tarsomere IV often smaller than others, especially in males (Fig. 3.7a–c) 7

6(5) Elytra, tergum XIII, and sternum VI together acuminate posteriorly (Fig. 3.6); pronotum not cordate (Fig. 3.2d); elytron without longitudinal sulci (Fig. 3.2d) . . . . . Methlini, *Celina*

6' Elytra, tergum XIII, and sternum VI not acuminate; pronotum strongly cordate (Fig. 3.2c); elytron with longitudinal sulci (Fig. 3.2c) . . .Hydroporini, Sternopriscina, *Carabhydrus*, 184

7(5) Eyes anteriorly rounded, not emarginate (Fig. 3.8a,b); males with ventral surface of pro- and often mesotarsomeres broadly expanded into a rounded (Fig. 3.7a) or transversely oval (Fig. 3.7b) palette with ventral adhesive setae; male median lobe symmetrical (Fig. 3.9a). 8

7' Eyes emarginate anterolaterally (Fig. 3.8c); males with ventral surface of pro- and mesotarsomeres expanded and bearing adhesive setae, but not together forming a transversely oval or rounded palette (Fig. 3.7c); male median lobe asymmetrical (Fig. 3.9b,c, in some cases not strongly so) 9

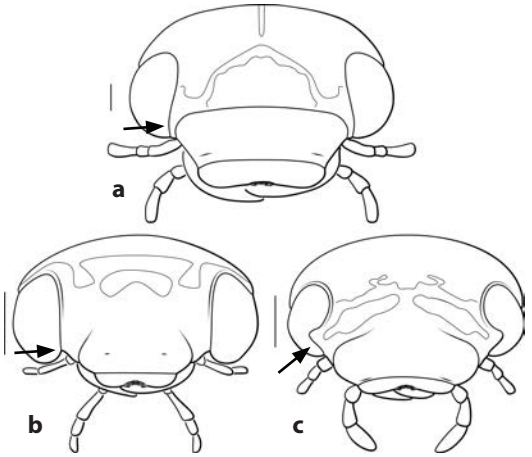


Fig. 3.8. Dytiscidae heads, anterior aspect. **a**, *Dytiscus verticalis*. **b**, *Acilius abbreviatus*. **c**, *Colymbetes exaratus*.

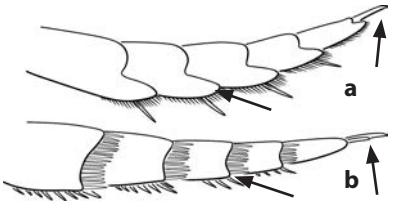


Fig. 3.5. Dytiscidae metatarsi. **a**, *Laccophilus proximus*. **b**, *Notaticus fasciatus.*

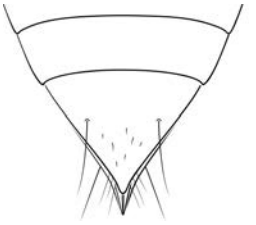


Fig. 3.6. *Methles cribratellus* abdominal apex, ventral aspect. Scale = 1.0mm.

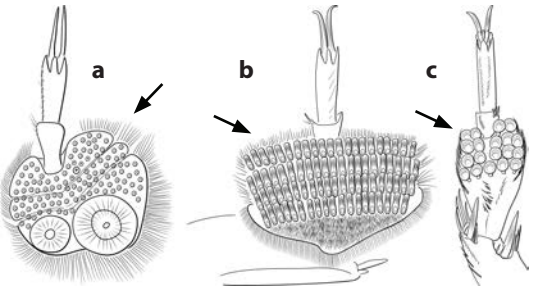


Fig. 3.7. Dytiscidae male protarsi, ventral aspect. **a**, *Dytiscus marginalis*. **b**, *Cybister* sp. **c**, *Colymbetes exaratus*.

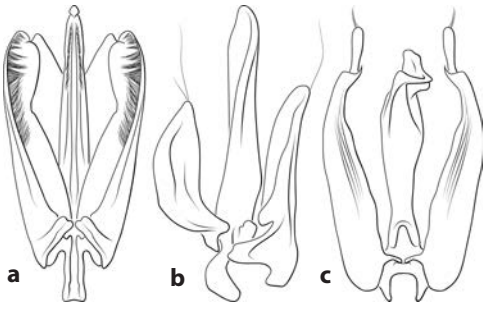


Fig. 3.9. Male aedeagi, dorsal aspect. **a**, *Dytiscus thianshanicus*. **b**, *Laccophilus maculosus*. **c**, *Copelatus* sp.

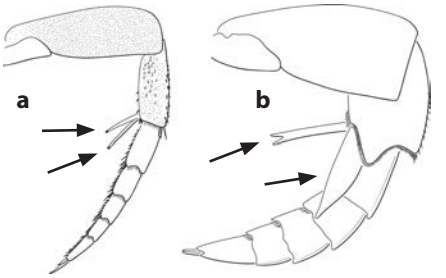


Fig. 3.10. Dytiscidae metalegs. **a**, *Acilius sulcatus*. **b**, *Megadytes lherminieri*.

8(7) Metatibial spurs similar in size and shape (Fig. 3.10a). . . . . Dytiscinae (in part), 111
8' Metatibial spurs different in size and shape, anterior spur wider, apically acuminate (Fig. 3.10b). . . . . Cybistrinae, 103

9(7) Metafemur with distinct linear series of setae near anteroapical angle (Fig. 3.11a), some species of *Platambus* and *Hydronebrius* (Agabinae) with posterior surface of metafemur densely sculptured and setae absent (see Fig. 8.4a), also *Hydrotrupes* with setae reduced to absent, but these beetles with labial palpi short and apical palpomere subquadrate (see Fig. 7.3a). . . . . .Agabinae, 55
9' Metafemur without distinct linear series of setae near anteroapical angle, though a small, nonlinear field of punctures or setae may be present in this location (Fig. 3.11b). 10

10(9) Prosternum medially and prosternal process with prominent longitudinal groove (Fig. 3.12a); anterior clypeal margin broadly emarginate medially (Fig. 3.13a) . . . . .Matinae, 50
10' Prosternum and prosternal process flattened or convex (Fig. 3.12b); anterior clypeal margin straight or concave (Fig. 3.13b). 11

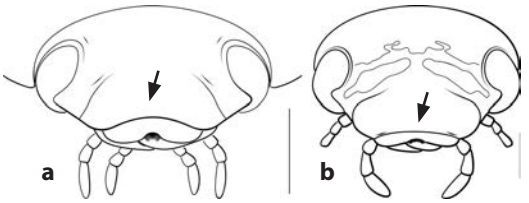


Fig. 3.13. Dytiscidae heads. **a**, *Batrachomatus daemeli*. **b**, *Colymbetes exaratus*. Scales = 1.0mm.

11(10) Metatarsal claws equal (Fig. 3.14a) or nearly equal (Fig. 3.14b) in length 12
11' Metatarsal claws distinctly unequal in length, posterior claw shorter than anterior claw (Fig. 3.14c). 16

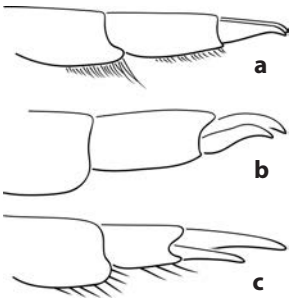


Fig. 3.14. Dytiscidae metatarsomeres and metatarsal claws. **a**, *Coptotomus longulus*. **b**, *Agabetes acuductus*. **c**, *Rhantus suturalis*.

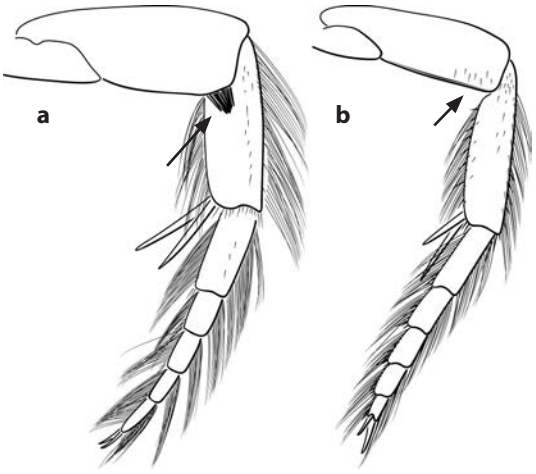


Fig. 3.11. Dytiscidae right metaleg. **a**, *Platynectes decimpunctatus*. **b**, *Rhantus suturalis*.

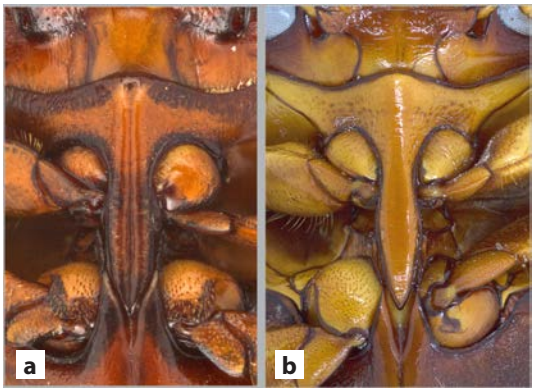


Fig. 3.12. Dytiscidae prosternal processes. **a**, *Matus bicarinatus*. **b**, *Hoperius planatus*.

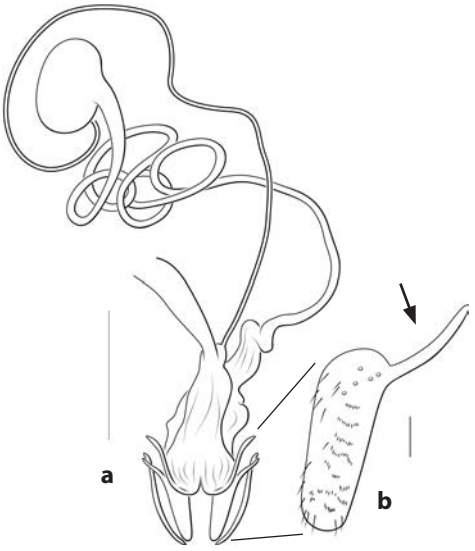


Fig. 3.15. *Hydrodytes inaciculatus* female reproductive tract. **a**, Ventral aspect. **b**, Left gongocoxa. Scales = 1.0mm (a) and 0.1mm (b).

12(11) Size <4mm in length; dorsal surface often with distinct opalescent sheen; gonocoxae broad, oval with prominent anteriorly directed apodeme (Fig. 3.15). . . . . Hydrodytinae, 135

12' Size generally larger, >4mm in length; dorsal surface not opalescent; if size small, then gonocoxae without prominent anteriorly directed apodeme (gonocoxae variable, long and slender or fused and knife-like) 13

13(12) Metacoxal lines either very closely approximated (Fig. 3.16a) or absent (Fig. 3.16b) . . . . . .Copelatinae, 78

13' Metacoxal lines distinctive, broadly separated, or subparallel (Fig. 3.16c) 14

14(13) Terminal maxillary and labial palpomeres distinctly biramous (Fig. 3.17a); prosternum with anterior margin extending ventrad from ventral surface of head, nearly vertical (Fig. 3.18a). . . . . Coptotominae, 133

14' Terminal palpomeres not biramous (Fig. 3.17b); prosternum with surface extending horizontally from posterior margin of head (Fig. 3.18b). 15

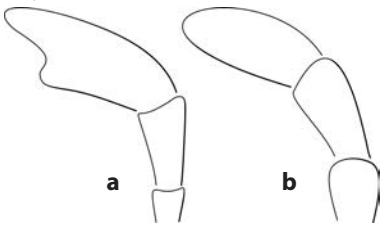


Fig. 3.17. Dytiscidae labial palpomeres. **a**, *Coptotomus longulus*. **b**, *Colymbetes exaratus*.

15(14) Dorsal surface variously modified, but not densely striolate; female gonocoxae apically rounded, not fused (as in Fig. 3.20a); habitus elongate, lateral margins distinctly discontinuous between pronotum and elytron (Fig. 3.21a); rare, found only in South American Andes, the Juan Fernandez Islands, and Tristan da Cunha . . . . . Colymbetinae (in part), 69

15' Dorsal surface densely striolate (Fig. 3.19); female gonocoxae fused and knife-like, rami fused and together serrated (Fig. 3.20b); habitus broadly oval, lateral margins approximately continuous between pronotum and elytron (Fig. 3.21b); eastern North America . . . . . Laccophilinae (in part), Agabetini, 89

16(11) Apices of elytra truncate or sinuate (Fig. 3.22a). . . . . .Lancetinae, 53

16' Apices of elytra evenly rounded, not truncate or sinuate (Fig. 3.22b). . . . . Colymbetinae (in part), 69

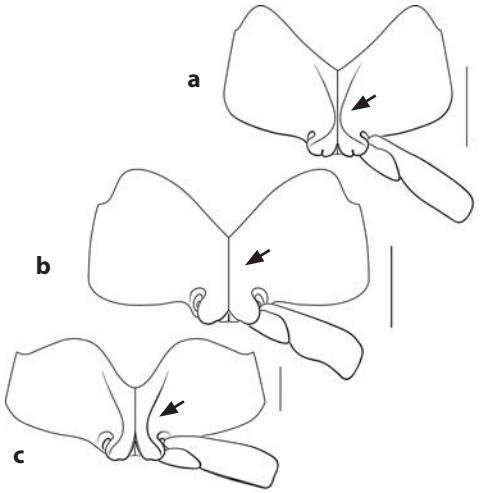


Fig. 3.16. Dytiscidae metacoxae and left metaleg. **a**, *Copelatus caelatipennis*. **b**, *Lacconectus regimbarti*. **c**, *Rhantus suturalis*. Scales = 1.0mm.

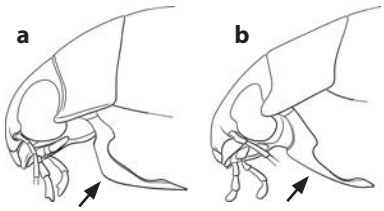


Fig. 3.18. Dytiscidae prosternal processes. **a**, *Coptotomus longulus*. **b**, *Colymbetes fuscus*.

Fig. 3.19. *Agabetes acuductus* dorsal surface.

Fig. 3.20. Dytiscidae female reproductive tract, ventral aspect. **a**, *Rhantus binotatus*. **b**, *Agabetes acuductus*. Scales = 1.0mm.

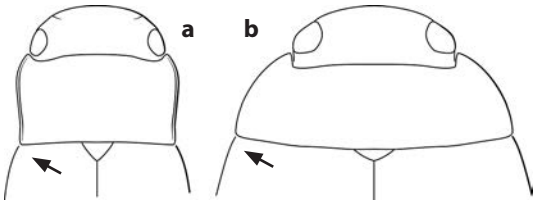


Fig. 3.21. Dytiscidae dorsal surfaces. **a**, *Rhantus selkirki*. **b**, *Agabetes acuductus*.

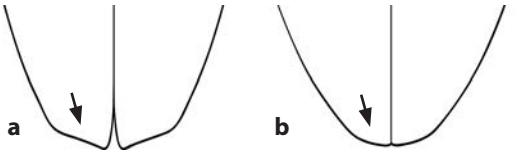


Fig. 3.22. Dytiscidae elytral apices. **a**, *Lancetes lanceolatus*. **b**, *Rhantus binotatus*.

Key to Larvae of the Subfamilies

Larvae of Dytiscidae are not comprehensively known, and it is likely that currently unknown larvae may not key out well. This is particularly true of Copelatinae, Agabinae, and Laccophilinae. These last two subfamilies, especially, seem to have overlapping variability that has not been clarified. First instar larvae are often fairly different from second and third instar larvae, but the following key should be adequate for all instars in most cases. Larvae of Hydrodytinae are not known.

1 Frontoclypeus anteriorly extended into elongated projection ("nasale" Fig. 3.23a); mandibles ventral to nasale distinctly curved dorsad (Fig. 3.23a); maxillary galea and palpifer absent (Fig. 3.24a); urogomphus two-segmented (Fig. 2.5l–o) . . . . . Hydroporinae, 138

1' Frontoclypeus not anteriorly extended, nasale absent (Fig. 3.23b); mandibles in horizontal plane, not curved dorsad (Fig. 3.23b); maxillary galea and palpifer present (Fig. 3.24b); urogomphus one- or two-segmented (see Fig. 2.5a–k) 2

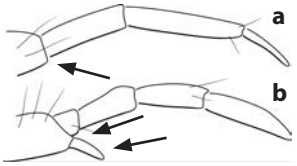


Fig. 3.24. Dytiscidae larval maxillary palpi. **a**, *Neoporus* sp. **b**, *Rhantus* sp.

2(1) Anteroventral margins of femora with natatory setae (Fig. 3.25a); lateral margins of abdominal segments VII and VIII with natatory setae (Fig. 3.26a,b) 3

2' Anteroventral margins of femora and tibiae without natatory setae (Fig. 3.25b); lateral margin of segment VIII with (Fig. 3.26c) or without (Fig. 3.26d) natatory setae 4

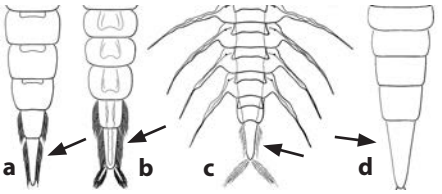


Fig. 3.26. Dytiscidae larval abdomens. **a**, *Megadytes* sp. **b**, *Dytiscus dauricus*. **c**, *Coptotomus* sp. **d**, *Agabetes acuductus*.

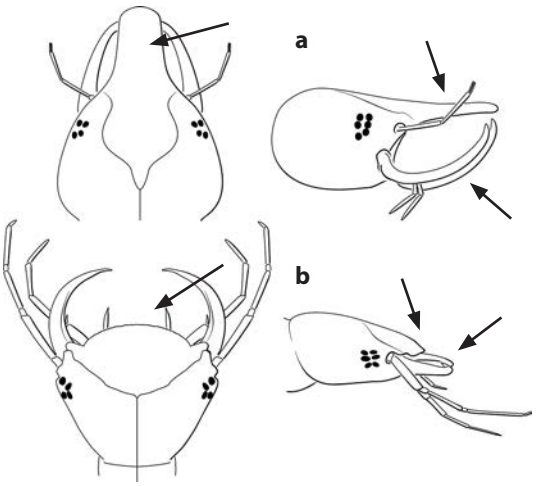


Fig. 3.23. Dytiscidae larval heads dorsal and lateral aspects. **a**, *Hydrovatus pustulatus*. **b**, *Dytiscus marginalis*.

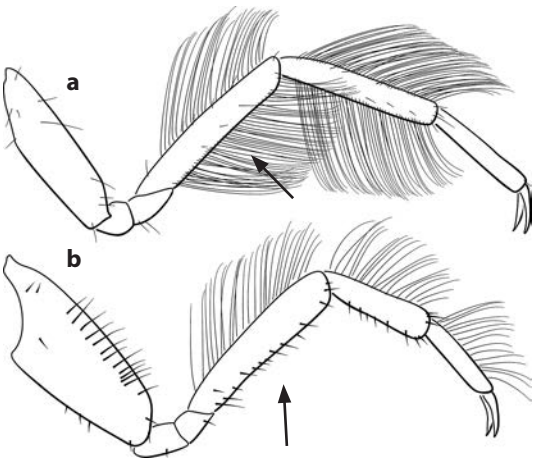


Fig. 3.25. Dytiscidae larval metalegs. **a**, *Dytiscus dauricus*. **b**, *Rhantus binotatus*.

3(2) Anterior margin of frontoclypeus trilobed (Fig. 3.27a); urogomphi small to minute (Fig. 3.26a) . . . . . .Cybistrinae, 103
3' Anterior margin of frontoclypeus evenly curved (Fig. 3.27b); urogomphi well developed (Fig. 3.26b) . . . . . Dytiscinae, 111

4(2) Each abdominal segment I–VI with an elongate, lateral tracheal gill on each side (Fig. 3.28a); frontoclypeus with a pronged extension anteromedially (Fig. 3.29a) . . . . . .Coptotominae, 133
4' Abdominal segments without lateral tracheal gills (Fig. 3.28b); frontoclypeus not extended anteromedially (Fig. 3.29b) 5

5(4) Mandibles medially distinctly serrated with large serrations, without medial groove (Fig. 3.30); maxillary galea hook-shaped (Fig. 3.31a); legs without natatory setae . . . . . Copelatinae, 78
5' Mandibles medially not serrated or only minutely serrated, with medial groove (*Hydrotrupes* without medial groove, but mandibles smooth medially): maxillary galea not hook-shaped (Fig. 3.31b); legs with or without natatory setae 6

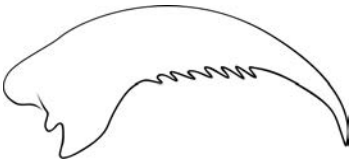


Fig. 3.30. *Copelatus* sp. larval mandible.

6(5) Urogomphi extremely short, indistinct (Fig. 3.34a) . . Laccophilinae (in part), Agabetini, 89
6' Urogomphi longer, distinct, well developed (Fig. 3.34b–f) 7

7(6) Urogomphi long and multisegmented (>2) (Fig. 3.34c) . . . . . Lancetinae, 53
7' Urogomphi one- or two-segmented (Fig. 3.34d–f) 8

8(7) Marginal spinulae present on the ventral surfaces of tarsal claws (Fig. 3.32); urogomphi one-segmented (Fig. 3.34d) . Colymbetinae, 69
8' Tarsal claws without ventral marginal spinulae; urogomphi one- or two-segmented (Fig. 3.34e,f) 9

Fig. 3.32. *Rhantus* sp. larval tarsomere and claw.

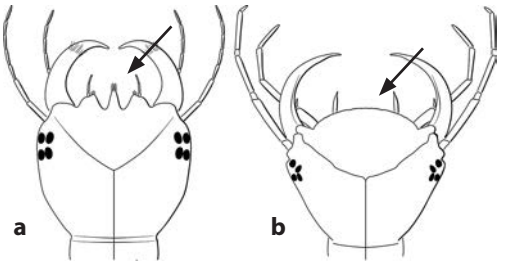


Fig. 3.27. Dytiscidae larval heads. **a**, *Megadytes* sp. **b**, *Dytiscus marginalis.*

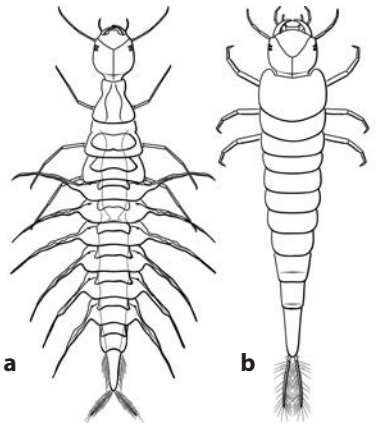


Fig. 3.28. Dytiscidae larvae. **a**, *Coptotomus* sp. **b,** *Rhantus suturalis*.

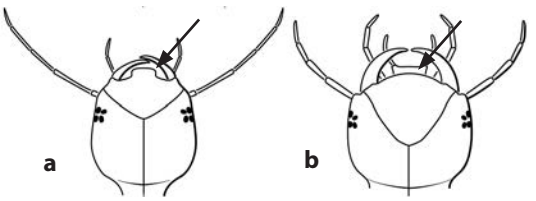


Fig. 3.29. Dytiscidae larval heads. **a**, *Coptotomus* sp. **b**, *Rhantus suturalis*.

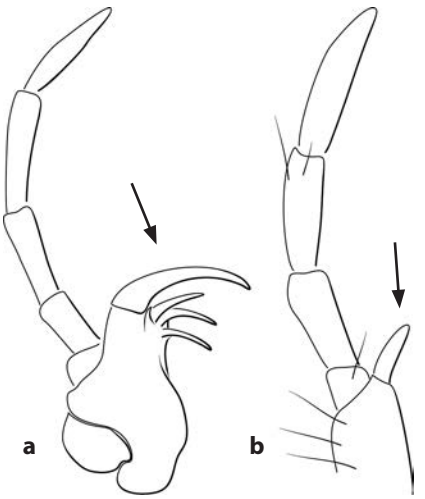


Fig. 3.31. Dytiscidae larval maxillae. **a**, *Copelatus* sp. **b**, *Rhantus* sp.

9(8) Urogomphus with few setae (Fig. 3.34e) . . . . . Agabinae, 55
9' Urogomphus with many setae (Fig. 3.34f) . 10

10(9) Antennae apically biramous (Fig. 3.33a) . . . . . .Laccophilinae, 87
10' Antennae apically uniramous (Fig. 3.33b) . . . . . Matinae, 50

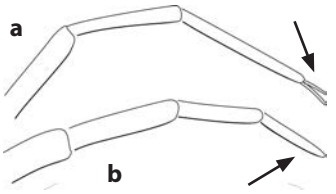


Fig. 3.33. Dytiscidae larval antennae. **a**, *Laccophilus* sp. **b**, *Matus* sp.

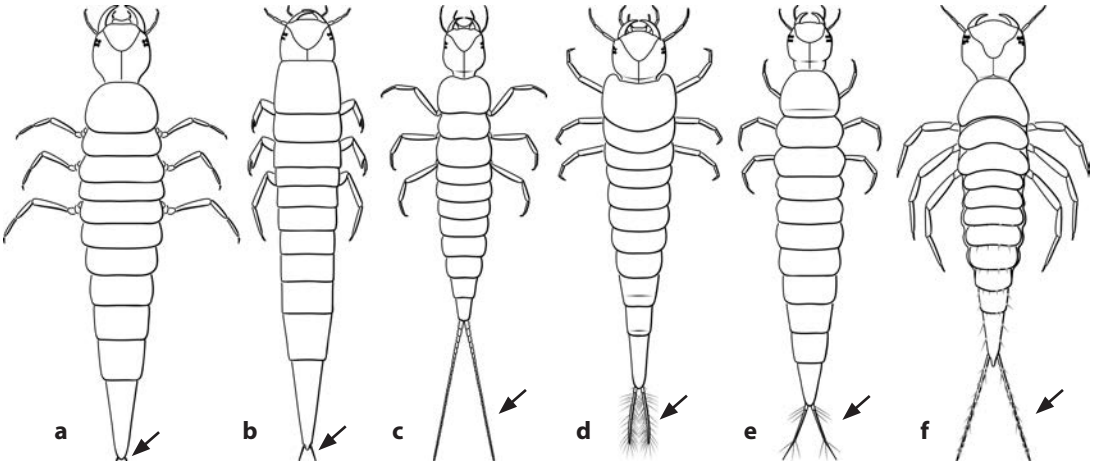


Fig. 3.34. Dytiscidae larvae. **a**, *Agabetes acuductus.* **b**, *Matus* sp. **c**, *Lancetes* sp. **d**, *Rhantus suturalis.* **e**, *Agabus* sp. **f**, *Laccophilus* sp.

Key to Subterranean and Terrestrial Genera

Subterranean diving beetles are found throughout the world and belong to many unrelated taxa, mostly in Hydroporinae but also Copelatinae. These species are highly convergent morphologically (Fig. 3.51), generally with the eyes reduced or absent, the cuticle depigmented, flightless with the elytra often fused and metathoracic wings reduced or absent, swimming setae reduced or absent, and often with the pronotum cordate, though the combination of these states varies across the taxa. Some terrestrial dytiscid taxa are similar. Because these species are so similar to each other, and are not similar to more "typical" epigaean species, their classification has been problematic. More recent molecular analyses have helped clarified the clades in which they belong even though they often do not have many of the diagnostic characteristics of those clades. Because of this, a separate key to the subterranean and terrestrial taxa is presented here. The key relies heavily on geographic distribution because of extreme difficulty in using morphology to diagnose these species. An additional potentially terrestrial genus in Bidessini, *Geodessus*, is not keyed here since it does not have typical terrestrial and subterranean features. Instead, it is included in the key to Bidessini.

1 Metacoxal lobes large, rounded, metafemur extending along dorsal margin of metatrochanter to metacoxa (Fig. 3.35a); metacoxal lines closely approximated (Fig. 3.35a); scutellum visible with elytra closed (Fig. 3.36a); medial surface of prosternum in same plane as prosternal process, not deflexed or declivous (Fig. 3.37a). . . . . Copelatinae, go to 2
1' Metacoxal lobes small or absent, metafemur separated from metacoxa by metatrochanter along dorsal margin (Fig. 3.35b); metacoxal lines variable, but not usually closely approxi-

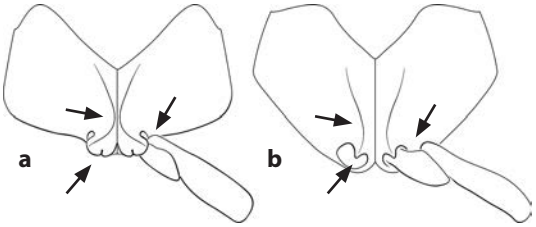


Fig. 3.35. Dytiscidae metacoxae, left metatrochanter and metafemur. **a**, *Copelatus* sp. **b**, *Psychopomporus felipi.*

mated medially; scutellum visible or not with elytra closed (Fig. 3.36b); medial surface of prosternum in different plane from prosternal process which is deflexed ventrally (Fig. 3.37b). . . . . .Hydroporinae, go to 3

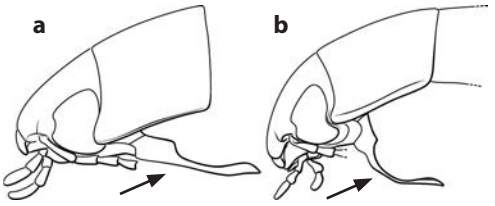


Fig. 3.37. Dytiscidae lateral surfaces. **a**, *Copelatus distinctus*. **b,** *Celina hubbelli.*

2(1) Found in Brazil . . . . . *Copelatus cessaima*, 82
2' Found in Australia
. . . . . *Exocelina abdita* and *E. rasjadi*, 84

3(1) Lateral lobes of male aedeagus with two segments (Fig. 3.38a); impressed line or plica on each side of middle of base of pronotum present (Fig. 3.39a) or absent (Fig. 3.39b)
. . . . . Bidessini, go to 4
3' Lateral lobes of male aedeagus with a single segment (Fig. 3.38b); impressed line or plica on each side of middle of base of pronotum absent (Fig. 3.39b) though a longer sublateral crease may be present on the disk on each side of pronotum (Fig. 3.43b). 9

4(3) Basal elytral striae absent (Fig. 3.39b) 5
4' Basal elytral striae present (Fig. 3.39a). 7

5(4) Metacoxal lines absent (Fig. 3.40a); China (Map 37.39). . . . . *Sinodytes hubbardi*, 253
5' Metacoxal lines present. 6

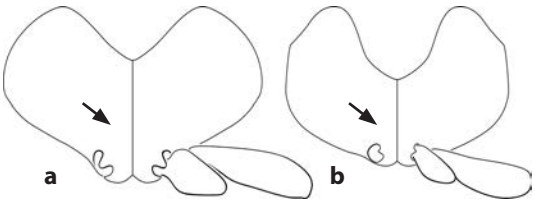


Fig. 3.40. Dytiscidae metacoxae, left metatrochanter and metafeumur . **a**, *Sinodytes hubbardi* (redrawn from Spangler, 1996). **b**, *Comaldessus stygius*.

6(5) Basal pronotal striae absent (Fig. 3.41a); Australian. . . . . *Neobidessodes*, 246
6' Basal pronotal striae present (Fig. 3.41b); Africa. . . . . *Uvarus chappuisi*, 256

7(4) Metacoxal lines absent (Fig. 3.40b); Texas, USA (Map 37.12) . .*Comaldessus stygius*, 235
7' Metacoxal lines present. 8

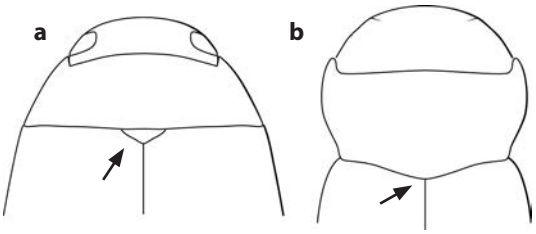


Fig. 3.36. Dytiscidae dorsal surfaces. **a**, *Copelatus* sp. **b**, *Haideoporus texanus.*

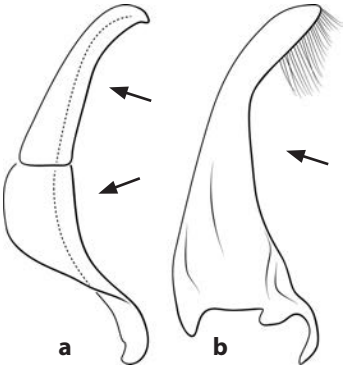


Fig. 3.38. Hydroporinae male lateral lobes. **a**, *Comaldessus stygius*. **b**, *Psychopomporus felipi.*

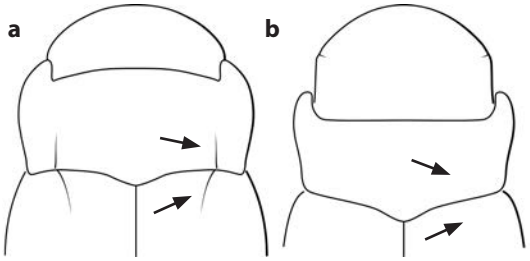


Fig. 3.39. Hydroporinae dorsal surfaces. **a**, *Sinodytes hubbardi* (redrawn from Spangler, 1996). **b**, *Comaldessus stygius.*

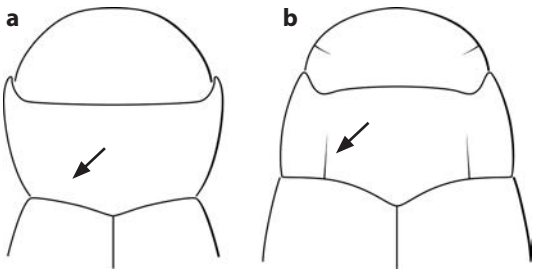


Fig. 3.41. Hydroporinae dorsal surfaces. **a**, *Neobidessodes limestoneensis* (redrawn from Watts and Humphreys, 2003). **b**, *Uvarus chappuisi* (redrawn from Peschet, 1932).

8(7) Male lateral lobe robust, apical segment broad, with elongate hook-shaped lobe (Fig. 3.42); Australian . . . . . *Limbodessus*, 244
8' Male lateral lobe slender, not broad, not with elongate hook-shaped lobe; Venezuela (Map 37.42). . . . . *Trogloguignotus concii*, 255

9(3) New World (North America) 10
9' Old World 13

10(9) Head unusually large relative to pronotum (Fig. 3.43a); elytra extending ventrally around abdomen (Fig. 3.44a); Texas, USA (Map 29.1) . . . . . Hydroporini, Siettitiina, *Ereboporus naturaconservatus*, 173
10' Head not unusually large relative to pronotum (Fig. 3.43b–d); elytra extending ventrally to lateral margins of abdomen (Fig. 3.44b) . . . 11

11(10) Pronotum laterally with distinct longitudinal impressions (Fig. 3.43b); western Oregon, USA (Map 29.11) . . . . . .Hydroporini, Siettitiina, *Stygoporus oregonensis*, 179
11' Pronotum laterally without longitudinal impressions (Fig. 3.43c,d) 12

12(11) Body outline distinctly discontinuous between pronotum and elytron (Fig. 3.43c); size larger (>3.2mm); Texas, USA (Map 27.1) . . . . . .Hydroporini, Hydroporina, *Haideoporus texanus*, 155
12' Body outline continuous between pronotum and elytron (Fig. 3.43d); size smaller (<2.1mm); Texas, USA (Map 29.7) . . . . .Hydroporini, Siettitiina, *Psychopomporus felipi*, 177

13(9) Australia region (Australia, New Caledonia, New Zealand) 14
13' Palearctic and Oriental 19

14(13) Terrestrial; with five distinctive costae on each elytron (Fig. 3.45a); distributed in New Caledonia (Map 23.5) . . . Hydroporinae, *incerta sedis*, *Typhlodessus monteithi*, 143
14' Subterranean; without costae on elytra (Fig. 3.45b). 15

15(14) New Zealand 16
15' Australia 17

Fig. 3.42. *Limbodessus compactus*, male lateral lobe.

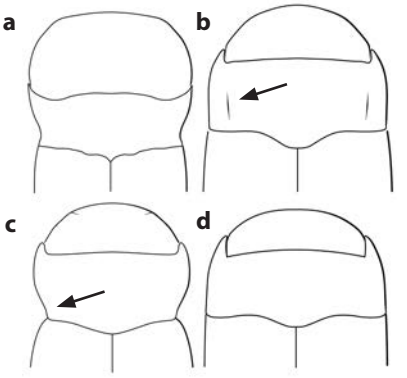


Fig. 3.43. Hydroporinae dorsal surfaces. **a**, *Ereboporus naturaconservatus*. **b**, *Stygoporus oregonensis*. **c**, *Haideoporus texanus*. **d**, *Psychopomporus felipi.*

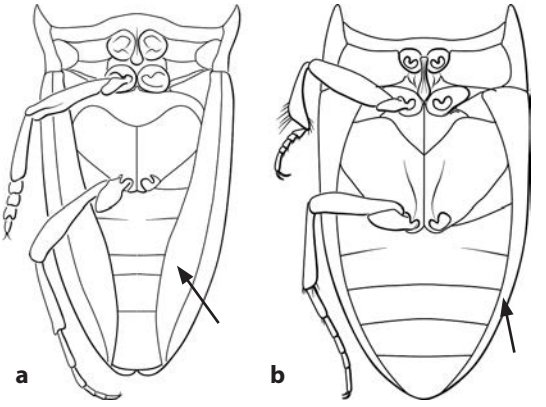


Fig. 3.44. Hydroporinae ventral surfaces. **a**, *Ereboporus naturaconservatus*. **b**, *Psychopomporus felipi.*

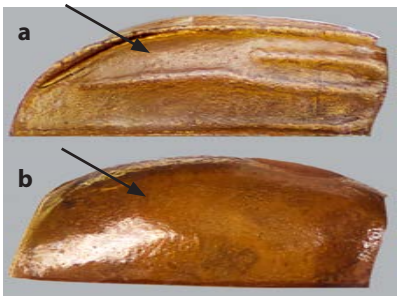


Fig. 3.45. Hydroporinae left elytron. **a**, *Typhlodessus monteithi*. **b**, *Siamoporus deharvengi*.

16(15) Pronotum posteriorly narrowed, body outline distinctly discontinuous between pronotum and elytron in dorsal aspect (Fig. 3.46a); New Zealand (Map 23.3)
. . Hydroporinae, *incerta sedis*, *Phreatodessus hades* and *P. pluto*, 142

16' Pronotum posteriorly not distinctly narrowed, body outline more continuous between pronotum and elytron in dorsal aspect (Fig. 3.46b); New Zealand (Map 23.1)
. . . Hydroporinae, *incerta sedis*, *Kuschelydrus phreaticus*, 141

17(15) Humeral angle of elytron broadly produced laterally, distinctly visible in dorsal aspect, lateral bead very broad (Fig. 3.47a); terrestrial, Australia (Map 30.8) . . *Paroster* (in part), 187

17' Humeral angle of elytron not produced laterally, lateral bead narrow (Fig. 3.47b,c); subterranean, found in groundwater
. . . . . Hydroporina, Sternopriscina 18

18(17) Scutellum visible with elytra closed (Fig. 3.47b). . . . . *Carabhydrus stephanieae*, 184

18' Scutellum not visible with elytra closed (Fig. 3.47c). . . . . *Paroster* (in part), 187

19(13) West Palearctic (European)
. . . . . Hydroporini, Siettitiina, go to 20
East Palearctic and Oriental. 23

20(19) With distinctive, longitudinal line on each side of pronotum (Fig. 3.48a,b). 21

20' Without longitudinal line on each side of pronotum (Fig. 3.48c,d) 22

21(20) Head very wide, laterally subangulate (Fig. 3.48a); pronotum and elytra with scattered, flattened setae (see Fig. 29.7); prosternal process apically contacting metaventrite; central Italy (Map 29.2). . . *Etruscodytes nethuns*, 174

21' Head regularly rounded (Fig. 3.48b); pronotum and elytra without pubescence (see Fig. 29.14); prosternal process apically narrowly separated from metaventrite; southern France (Map 29.9)
. .*Siettitia avenionensis* and *S. balsetensis*, 178

22(20) Pronotum cordate, widest anterior to middle (Fig. 3.48c); eyes absent (Fig. 3.48c); southern Iberia (Map 29.4). .*Iberoporus cermenius*, 175

22' Pronotum not cordate, laterally rounded, widest medially (Fig. 3.48d); eyes small (Fig. 3.48d); Morocco . . *Graptodytes eremitus*, 174

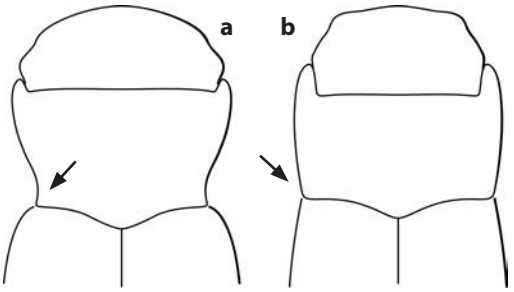


Fig. 3.46. Hydroporinae dorsal surfaces. **a**, *Phreatodessus hades*. **b**, *Kuschelydrus phreaticus.*

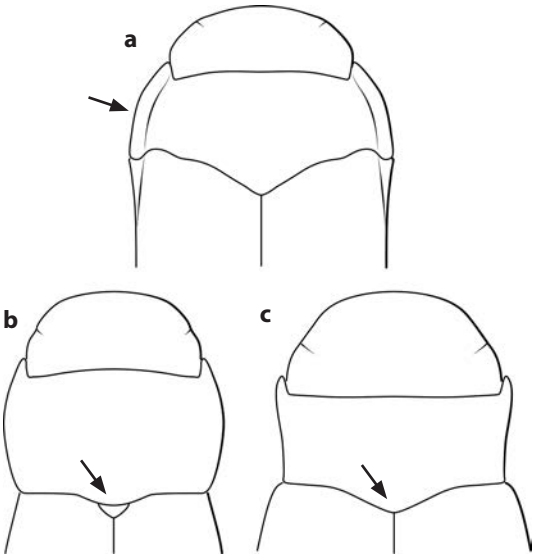


Fig. 3.47. Hydroporinae dorsal surfaces. **a**, *Paroster caecus*. **b**, *Carabhydrus stephanieae*. **c**, *Paroster readi.*

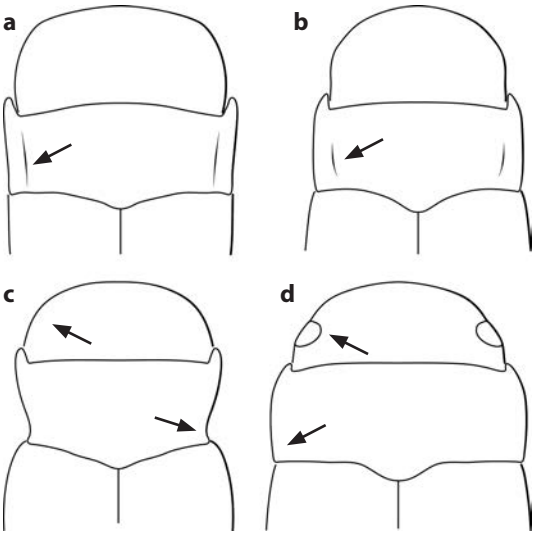


Fig. 3.48. Hydroporinae dorsal surfaces. **a**, *Etruscodytes nethuns*. **b**, *Siettitia avenionensis*. **c**, *Iberoporus cermenius*. **d**, *Graptodytes eremitus*.

23(19) Found in Japan 24
23' Found in China and Thailand 25

24(23) Metacoxal lobes reduced, base of metatrochanter nearly completely exposed (Fig. 3.49a); body globular and robust (see Fig. 36.19); Japan (Map 36.8)
. . . . . Hyphydrini, *Dimitshydrus typhlops*, 214
24' Metacoxal lobes larger, covering basal portion of metatrochanter (Fig. 3.49b); body elongate (Fig. 23.15); Japan (Map 23.2)
. Hydroporinae, *incerta sedis*, *Morimotoa*, 142

25(23) Size small (<2.5mm); pronotum not cordate (Fig. 3.50a); China
. . . . . Hyphydrini, *Microdytes trontelji*, 217
25' Size large (>3.0mm); pronotum cordate (Fig. 3.50b); Thailand (Map 26.1)
. . . . Hydroporinae, *incerta sedis*, *Siamoporus deharvengi*, 152

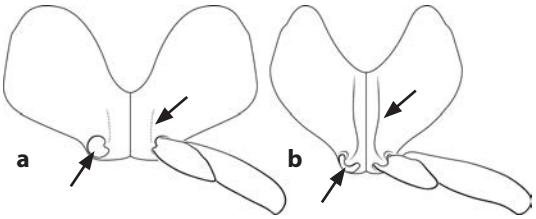


Fig. 3.49. Dytiscidae metacoxa, left metatrochanter and metafemur. **a**, *Dimitshydrus typhlops*. **b**, *Morimotoa phreatica*.

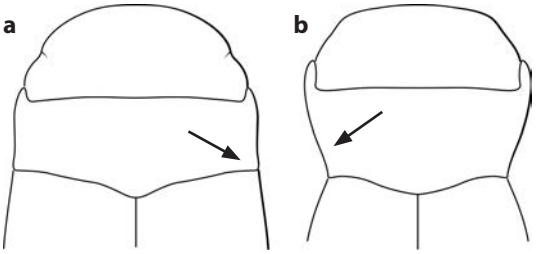


Fig. 3.50. Hydroporinae dorsal surfaces. **a**, *Microdytes trontelji*. **b**, *Siamoporus deharvengi*.

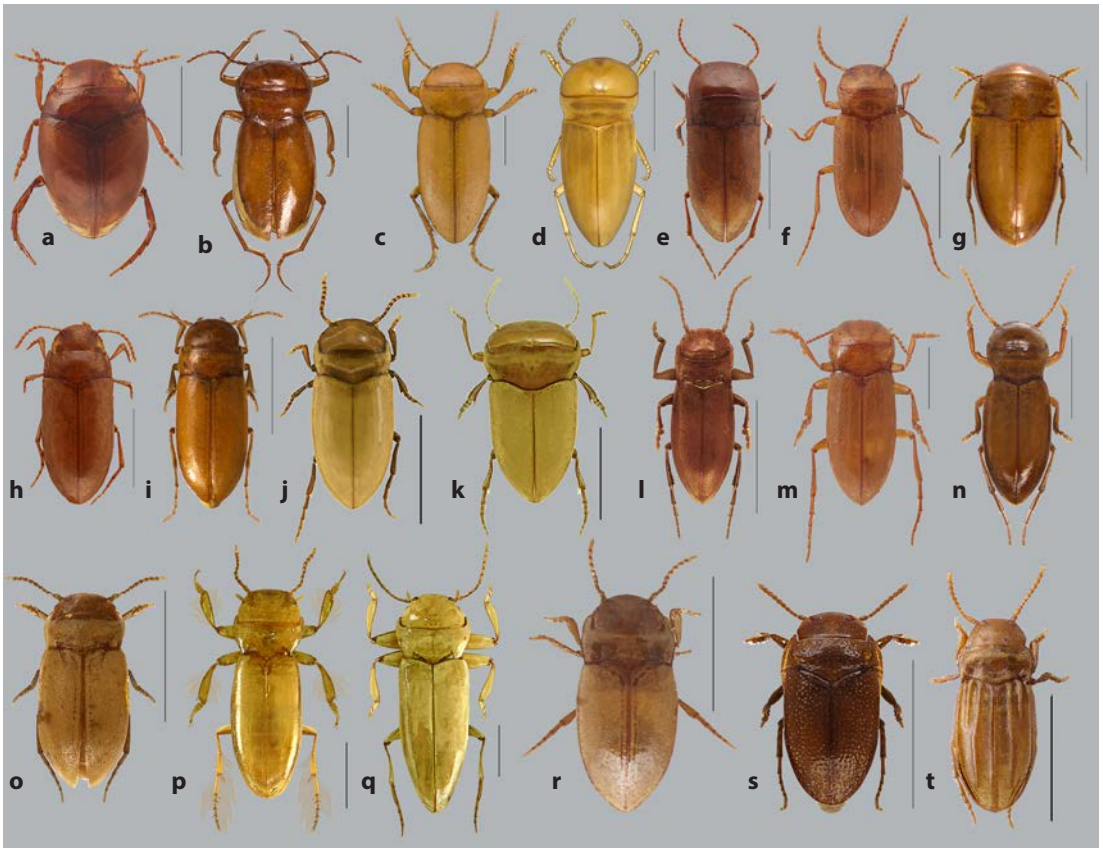


Fig. 3.51. Subterranean (a–r) and terrestrial (s,t) diving beetles. **a**, *Dimitshydrus typhlops*. **b**, *Siamoporus deharvengi*. **c**, *Haideoporus texanus*. **d**, *Ereboporus naturaconservatus*. **e**, *Etruscodytes nethuns*. **f**, *Iberoporus cermenius*. **g**, *Psychopomporus felipi*. **h**, *Siettitia avenionensis*. **i**, *Stygoporus oregonensis*. **j**, *Paroster napperbyensis*. **k**, *P. macrocephalus*. **l**, *Kuschelydrus phreaticus*. **m**, *Morimotoa phreatica*. **n**, *Phreatodessus hades*. **o**, *Comaldessus stygius*. **p**, *Limbodessus macroloraensis*. **q**, *L. macrotarsus*. **r**, *Trogloguignotus concii*. **s**, *Paroster caecus*. **t**, *Typhlodessus monteithi*. Scales = 1.0mm.

4. Subfamily Matinae

Body Length. 5.4–9.6mm.

Diagnosis. This subfamily includes Dytiscidae with the following character combination: (1) the medial portion of the prosternum and prosternal process is distinctly longitudinally sulcate (Fig. 4.1); (2) the anterior clypeal margin is strongly curved (Fig. 4.2); (3) the anterodorsal margins of metatarsomeres I–IV are lobed (Fig. 4.4); and (4) the female genitalia are the "amphizoid-type" of configuration (Miller, 2001c) with a large accessory gland reservoir attached to the fertilization duct (Fig. 4.3).

Classification. Sharp (1882) placed the members of this group in a cluster of seven "unassociated" genera of "Colymbetides." Matines were thereafter placed as a tribe of Colymbetinae until Miller (2001c) elevated the group to subfamily rank. Miller (2001c) found the group sister to all other diving beetles, though the analysis by Ribera *et al.* (2008) resulted in matines in a clade with Hydrodytinae, Lancetinae, and Dytiscini. Miller and Bergsten (2014a) found Matinae to be monophyletic and sister to the rest of Dytiscidae with strong support, corroborating Miller (2001c). Relationships among matine genera, based on larval characters, were investigated by Alarie *et al.* (2001b). A recent revision of the Australian taxa resulted in synonymy of *Allomatus* Mouchamps with *Batrachomatus* Clark (Hendrich and Balke, 2013).

Fig. 4.1. *Matus ovatus*, prosternum and prosternal process.

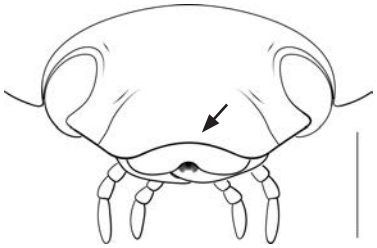


Fig. 4.2. *Batrachomatus daemeli* head, anterior aspect. Scale = 1.0mm.

Diversity. There are now two genera in the group, *Batrachomatus* and *Matus*.

Natural History. *Matus* are characteristic of lentic or slow lotic habitats, including *Sphagnum* bogs, whereas *Batrachomatus* tend to be in the margins of lotic habitats in detritus.

Distribution. This group has a relictual disjunct distribution with *Matus* found in eastern North America and *Batrachomatus* found in Australia.

Fig. 4.3. *Matus ovatus*, female reproductive tract, ventral aspect. Scale = 1.0mm.

Key to the Genera of Matinae

1 Metatarsal claws short and curved, subequal or slightly unequal in length (Fig. 4.4a); Australia (Map 4.1) . . . . . *Batrachomatus*, 51

1' Metatarsal claws elongate and nearly straight, distinctly unequal in length (Fig. 4.4b); eastern Nearctic (Map 4.2). . . . . *Matus*, 51

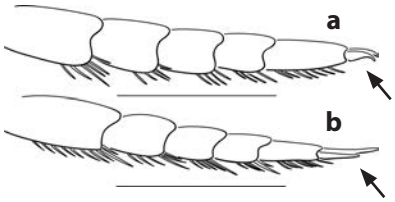


Fig. 4.4. Matinae, metatarsus. **a**, *Batrachomatus daemeli*. **b**, *Matus bicarinatus*. Scales = 1.0mm.

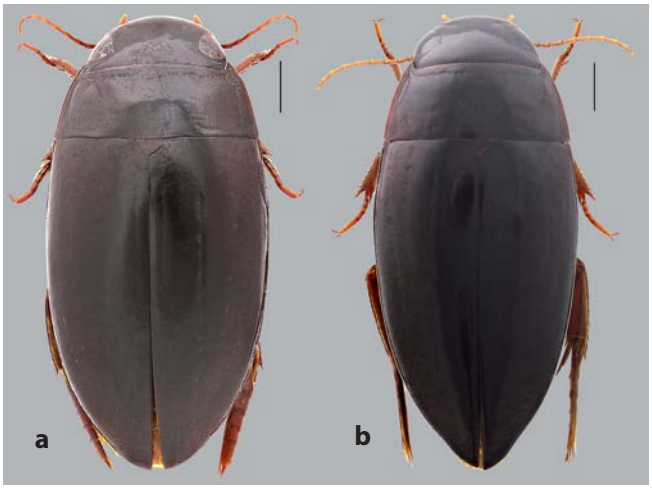


Fig. 4.5. *Batrachomatus* species. **a**, *B. daemeli*; **b**, *B. nannup*. Scales = 1.0mm.

Genus *Batrachomatus* Clark, 1863

Body Length. 6.9–9.6mm.

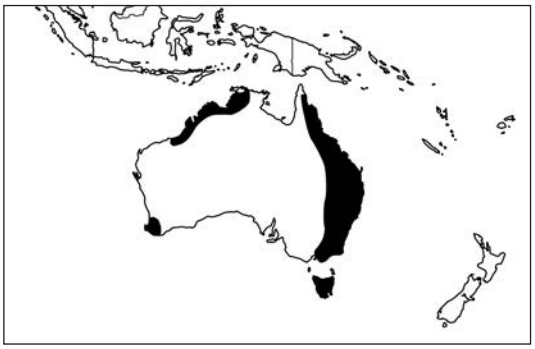
Diagnosis. This genus differs from *Matus* in having the dorsal surface microreticulate or densely punctate (or both) and metatarsal claws short, curved, and subequal or slightly unequal in length (Fig. 4.4a). *Batrachomatus* are typically dark reddish-black to black (Fig. 4.5), with some specimens marked with longitudinal reddish or yellowish-red stripes laterally on the elytra.

Classification. *Batrachomatus* were placed in the genus *Matus* by Sharp (1882), which is now restricted to North America, though the two genera are similar. Another genus, *Allomatus* Mouchamps, historically included two species (Watts, 1978) and was based on presence of reticulate surface sculpturing instead of dense punctures as in *Batrachomatus*. A recent phylogenetic revision of the Australian species resulted in synonymization of *Allomatus* with *Batrachomatus* based on analysis of DNA sequence data and a newly discovered species, *B. larsoni* Hendrich and Balke, that has the dorsal surface both microreticulate and punctate (Hendrich and Balke, 2013).

Diversity. There are currently five species placed in *Batrachomatus* that can be identified using the revision by Hendrich and Balke (2013).

Natural History. Members of this genus are characteristic inhabitants of relatively low-gradient streams, where they occur in detritus and plant materials, under stones, or in hanging root mats under overhangs along the margins. Additional detailed habitat information is provided by Hendrich and Balke (2013). Larvae were described by Alarie *et al.* (2001b) and Alarie and Butera (2003).

Distribution. Members of this group are found in streams in northern, eastern, and southwestern Australia (Map 4.1).



Map 4.1. Distribution of *Batrachomatus*.

Genus *Matus* Aubé, 1836

Body Length. 5.4–9.4mm.

Diagnosis. *Matus* have the dorsal surface distinctly and finely microreticulate combined with straight and distinctly unequal length metatarsal claws (Fig. 4.4b). This combination does not occur in *Batrachomatus*. Specimens are reddish or reddish-black and medium sized (Fig. 4.6).

Classification. Sharp (1882) included the Australian species of Matinae in his concept of the genus, but

Fig. 4.6. *Matus bicarinatus*. Scale = 1.0mm.

Matus is today restricted to North America.

Diversity. There are four recognized species and one subspecies in this group, which can be identified using the key in Larson *et al.* (2000). The taxonomy of the group was earlier also treated by Leech (1941b) and Young (1953).

Natural History. Unlike the Australian Matinae, most members of *Matus* are typical of lentic rather than lotic habitats with most specimens found in *Sphagnum* bogs (Young, 1953), though some can be found in backwater areas of slow streams. Immature stages have been described by Alarie and Butera (2003), Alarie *et al.* (2001b), and Wolfe and Roughley (1985). Larvae of some species have characteristic chelate (claw-shaped) protarsi (J. Balfour-Browne, 1947b; Alarie *et al.*, 2001b), unusual for diving beetles and even for insects, though not all *Matus* species have this (Alarie and Butera, 2003).

Distribution. This group is found in eastern North America from southern Canada to Florida and west to Texas (Map 4.2).

Map 4.2. Distribution of *Matus*.

5. Subfamily Lancetinae

Body Length. 7.5–12mm.

Diagnosis. The single genus in this subfamily, *Lancetes* Sharp, has a combination of both apomorphic and plesiomorphic states within Dytiscidae, and can be distinguished by the following: (1) the elytral apices are sinuate or subtruncate (Figs. 5.1b,2); (2) the female reproductive tract includes two genital openings as well as a distinctive bursa, and a spermathecal duct extending from the anterior apex of the bursa (Fig. 5.1c); (3) the female gonocoxae are weakly, but distinctly fused dorsally (Fig. 5.1c); (4) the median lobe is asymmetrical with a distinct, elongate ventral sclerite (Fig. 5.1d); and (5) the metatarsal claws are unequal in length in both sexes (Fig. 5.1e). Members of this group are medium sized, elongate, and streamlined (Fig. 5.2). The elytra are often irrorate or, more rarely, longtitudinally fasciate (Fig. 5.2).

Classification. The genus was originally described by Sharp (1882) and was placed in a group with six other "unassociated" dytiscid genera, including *Agabetes*, *Matus*, *Coptotomus,* and others in "Colymbetides." *Lancetes* was regarded as potentially closely related to *Coptotomus* (as a tribe Coptotomini of Colymbetinae) by Brinck (1948). Nilsson (1989b) tentatively suggested a close relationship between the genus *Lancetes* and Laccophilinae (including *Agabetes*) based in part on the common presence of natatory setae on the dorsal and ventral margins of the metatarsus but only the dorsal margin of the metatiba in both sexes (Fig. 5.1a). Others have suggested a close relationship between Lancetinae and Dytiscinae based on adult (Ruhnau and Brancucci, 1984; Miller, 2001c) and larval (Alarie *et al.*, 2002a) characters. Although not strongly supported in their analysis, Ribera *et al.* (2008) found Lancetinae together with Dytiscini, Hydrodytinae, and Matinae as sister to the rest of Dytiscidae. Most recently, Miller and Bergsten (2014a) found a monophyletic Lancetinae, sister to Agabinae + Colymbetinae but with weak support.

Diversity. *Lancetes* is the only lancetine genus.

Natural History. See below under *Lancetes*.

Distribution. See below under *Lancetes*.

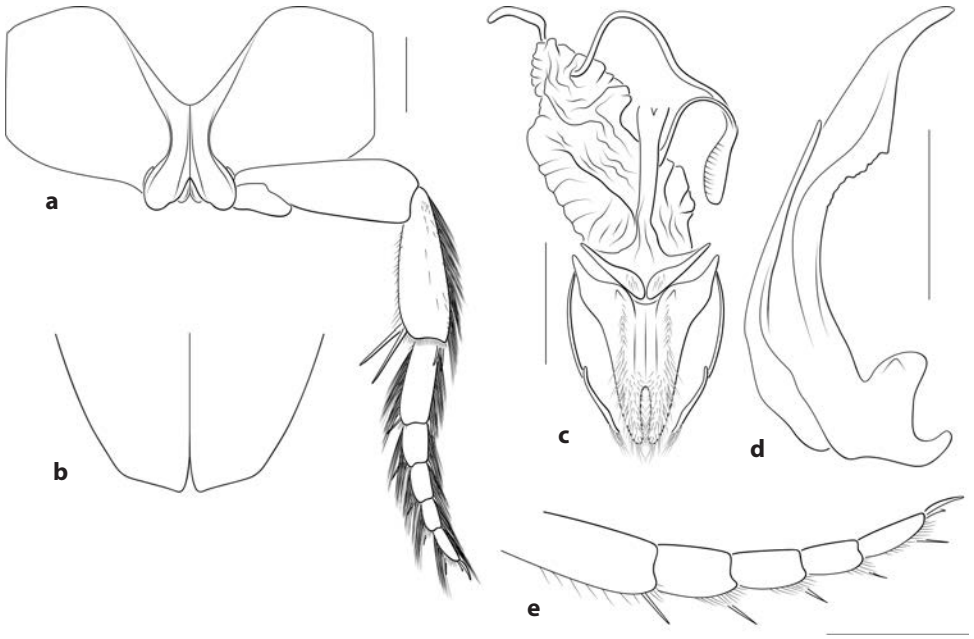


Fig. 5.1. *Lancetes* sp. features. **a**, *L. lanceolatus*, metacoxae and left metaleg. **b**, *L. lanceolatus* elytral apices. **c**, *L. nigriceps* female reproductive tract, ventral aspect. **d**, *L. nigriceps* median lobe, right lateral aspect. **e**, *L. lanceolatus* metatarsusv. Scales = 1.0mm.

Genus *Lancetes* Sharp, 1882

Diagnosis. This is the only lancetine genus and is characterized by its diagnosis (see above).

Classification. See above for discussion of classification of the single genus, *Lancetes*.

Diversity. There are currently 22 species in *Lancetes* (Nilsson, 2015). Since Sharp (1882) first treated the

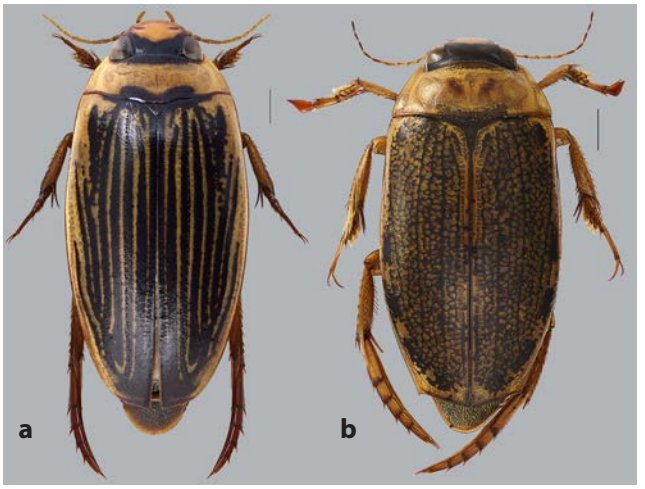
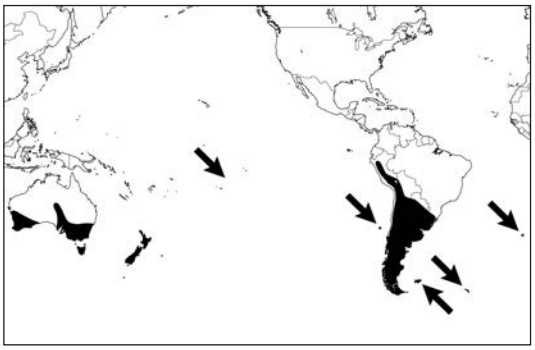


Fig. 5.2. *Lancetes* species. **a**, *L. lanceolatus*. **b**, *L. nigriceps*. Scales = 1.0mm.

group it has been revised in whole or in part by Zimmermann (1924), Ríha (1961), and Bachmann and Trémouilles (1981). The single Australian species, *L. lanceolatus* (Clark), was treated by Watts (1978).

Natural History. The Australian species is characteristic of temporary or permanent shallow lentic habitats, often occurring in very large numbers. The New World species occur in streams and pools in temperate or high-elevation South America and live at some of the highest elevations of any diving beetles. Several aspects of their life history, larval and pupal stages, and ecology have been investigated (Beir, 1928; Cekalovic-Kuschevich and Spano, 1981; Nicolai and Droste, 1984; Ruhnau and Brancucci, 1984; Brancucci and Ruhnau, 1985; Alarie *et al.*, 2002a; Michat *et al.*, 2005). Studies include several investigations of their involvement in sub-Antarctic ecology (Nicolai and Droste, 1984; Arnold and Convey, 1998; Hansson and Tranvik, 2003).

Distribution. Members of this genus have a disparate, Gondwanian distribution with one species, *L. lanceolatus*, found throughout southern Australia and New Zealand, and most other species in the genus in temperate southern South America and at high elevation in the Andes north through Peru (Map 5.1). Some species occur in some of the most remote localities for any diving beetle, or indeed insects in general, including Tierra del Fuego (Sharp, 1882), South Georgia Island (Müller, 1884; Gressitt, 1970; Nicolai and Droste, 1984; Arnold and Convey, 1998; Hansson and Tranvik, 2003), Tristan da Cuhna (Brinck, 1948), and the King George Islands (Régimbart, 1887) (Map 5.1).



Map 5.1. Distribution of *Lancetes*.

6. Subfamily Agabinae

Body Length. 4.0–14.5mm.

Diagnosis. Agabinae includes Dytiscidae with a linear series of closely spaced setae at the anteroventral angle of the metafemur (Fig. 6.1a). The series of setae is absent in some specimens of *Hydrotrupes*, *Hydronebrius,* and some *Platambus*, but these are evidently secondary losses (Nilsson, 2000; Ribera *et al.*, 2004). Other dytiscids, such as many Colymbetinae, have metafemoral setae, but not a linear series of closely spaced, stiff setae as in Agabinae. Also, agabines have the anterior margin of the eyes emarginate (Fig. 6.2). The metatarsal claws of most groups are subequal in length (Fig. 6.1b), but others (e.g., many *Ilybius*) are distinctly unequal (Fig. 6.1c). The male lateral lobes are symmetrical, and the median lobe is bilaterally asymmetrical (Fig. 6.1d), though in some groups (e.g., again, many *Ilybius*) the median lobe is nearly symmetrical (Fig. 6.1e). A great majority of these beetles are approximately oval, medium sized, and brown, testaceous, or black without very distinctive color patterns. There are numerous exceptions, however, with a moderate size range and a variety of maculate, striped, or otherwise patterned species.

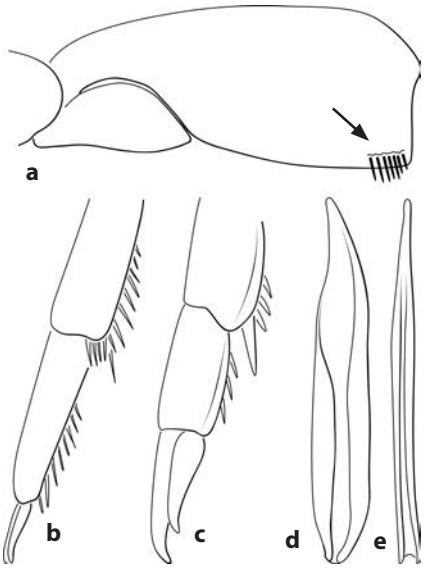


Fig. 6.1. Agabinae features. **a**, *Ilybius biguttulus*, right metatrochanter and metafemur. **b**, *Agabus griseipennis*, metatarsal claws. **c**, *I. picipes*, metatarsal claws. **d**, *A. confinis*, male median lobe, ventral aspect. **e**, *I. biguttulus*, male median lobe, ventral aspect. Scales = 1.0mm.

Classification. Agabinae has usually been recognized as a tribe within Colymbetinae until Miller (2001c) found it unrelated to them and elevated it to subfamily rank. This was further confirmed by Ribera *et al.* (2002b; 2008), who in addition found Agabinae to be paraphyletic with the *Platynectes*-group of genera not related to the *Agabus*-group. Roughley (2000) placed the anomalous genus, *Hydrotrupes*, in its own subfamily based on larval features presented by Beutel (1994) and suggested that it is sister to all Dytiscidae except Copelatinae. This was not supported by Miller's (2001c) analysis of adult morphological features or Alarie's *et al.* (1998) analysis of larval characters, each of whom found *Hydrotrupes* related to agabines. Ribera *et al.* (2008) found *Hydrotrupes* resolved together with the *Platynectes*-group of genera. A more focused analysis on the subfamily by Ribera *et al.* (2004) also supported a distinction between the *Agabus*-group of genera and the *Platynectes*-group (which included *Hydrotrupes*). The recent analysis by Miller and Bergsten (2014a) resolved both the *Agabus*-group and *Platynectes*-group (the latter including *Hydrotrupes*) as monophyletic, with each of the two groups also together monophyletic. To reflect this resolution, the classification was changed to recognize one subfamily, Agabinae, with two tribes, Agabini and Hydrotrupini. They found the subfamily to be sister to Colymbetinae (Miller and Bergsten, 2014a).

Agabini (the *Agabus*-group) includes primarily Holarctic taxa whereas Hydrotrupini (the *Platynectes*-group) includes several genera from northern and high-elevation South America, Central America, Southeast Asia and Australia, and the North American and Chinese genus *Hydrotrupes* (Ribera *et al.*, 2004; 2008; Miller and Bergsten, 2014a). *Hydronebrius* has been historically placed in its own tribe, Hydronebriini Brinck, based on absence of the metafemoral series of setae. Nilsson (2000) suggested its absence to be the result of increased punctation on the metafemur and synonymized the tribe with Agabini *sensu lato*.

Diversity. Agabinae includes two tribes, Agabini and Hydrotrupini, with altogether 11 genera.

Natural History. This is an impressively speciose group with members in many habitats, including lentic and lotic water bodies with many specific to certain microhabitats. Some are in hygropetric habitats, boreal bogs, rocky streams, and others.

Distribution. In aggregate, this subfamily occurs throughout much of the world though species are largely absent in lowland areas of South America and Africa.

Key to the Tribes of Agabinae

1 With elliptical, sublateral foveae on clypeus (Fig. 6.2a); both males and females with natatory setae along ventral margins of metatibia and metafemur (Fig. 6.3a, natatory setae absent in *Hydrotrupes* (see Fig. 7.2c), which has distinctly quadrate apical labial palpomeres (see Fig. 7.3a) . . . . . Hydrotrupini, 57

1' With narrow, linear foveae along anterolateral angles of clypeus (Fig. 6.2b) or with marginal groove across entire clypeus (Fig. 6.2c); females without any natatory setae along ventral margins of both metatibia and metafemur (Fig. 6.3b, except in one species, *Ilybius discedens* Sharp, which has the metatarsal claws distinctly unequal in length) . . . . . Agabini, 62

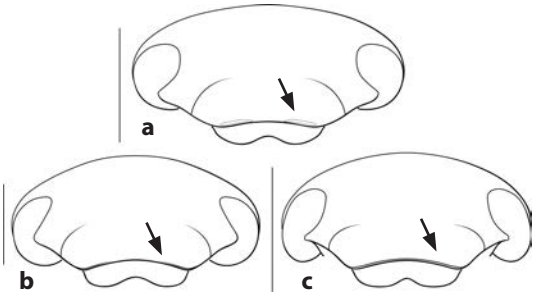


Fig. 6.2. Agabinae heads, anterior aspect. **a**, *Platynectes reticulosus*. **b**, *Ilybiosoma lugens*. **c**, *Agabus obliteratus*. Scales = 1.0mm.

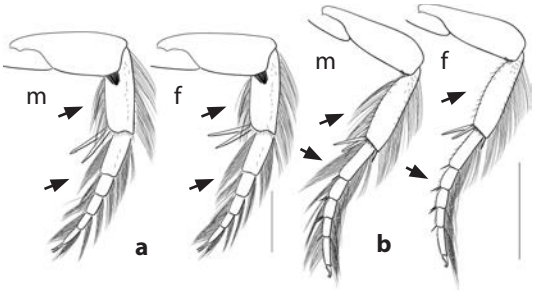


Fig. 6.3. Agabinae metalegs, male and female. **a**, *Platynectes decempunctatus*. **b**, *Agabus obliteratus*. Scales = 1.0mm.

7. Tribe Hydrotrupini

Body Length. 4–10.7mm.

Diagnosis. Hydrotrupini are Agabinae with the following combination: (1) sublateral elliptical foveae present on the clypeus (Fig. 7.1, somewhat ambiguous in *Hydrotrupes*) and (2) females with natatory setae along the ventral margins of the metatibia and metafemur (Fig. 7.2a,b, natatory setae entirely absent in *Hydrotrupes*, Fig. 7.2c). Male diving beetles often have natatory setae on the ventral margins of the metatibia and metafemur, but females of many groups do not. Within Agabinae, only hydrotrupines have ventral setae in both males and females with the exception of one Agabini species, *Ilybius discedens* Sharp, which is clearly derived within that tribe (Larson, 1987; Nilsson, 1996a; 2000).

Classification. The species *Hydrotrupes palpalis* Sharp was historically placed in Agabini (Sharp, 1882), but Beutel (1994), based upon certain larval characters, concluded the genus is not near Agabini or Colymbetinae, but probably sister to a much larger group of Dytiscidae. Based on this evidence, Roughley (2000), not without reservation, erected Hydrotrupinae to include the species. Other evidence, both from larval (Alarie *et al.*, 1998) and adult (Miller, 2001c) morphology, suggests instead that *Hydrotrupes* is an agabine. Recent, more comprehensive analyses (Ribera *et al.*, 2008; Miller and Bergsten, 2014a) resolve *Hydrotrupes* together with several Agabini genera related to *Platynectes*, the "Austral agabines." These genera were together placed in a tribe by Miller and Bergsten (2014a).

Diversity. Hydrotrupini includes five genera.

Natural History. Most species in this group occur in streams or springs. Several members of the group, such as certain species in *Platynectes* and *Leuronectes*, are characteristic of small, often leaf-choked rock pools or hygropetric habitats, including rock-face seeps. *Hydrotrupes* is perhaps the best known inhabitant of these situations, occurring in seeps in coastal areas of western North America, and possibly in similar habitat in China (see below under *Hydrotrupes*). Other Hydrotrupini live in forest pools, springs, and small stream margins.

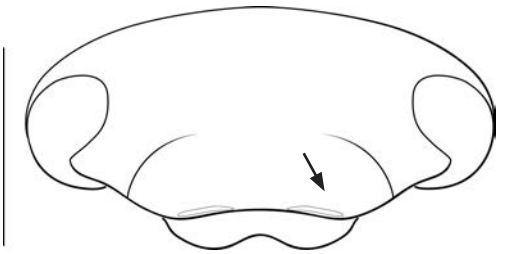


Fig. 7.1. *Platynectes decempunctatus* head, anterior aspect. Scale = 1.0mm.

Distribution. This is a primarily austral group with representatives in lowland South America, Australia, and Southeast Asia with the only northerly occurring group, *Hydrotrupes*, found in China and the western Nearctic.

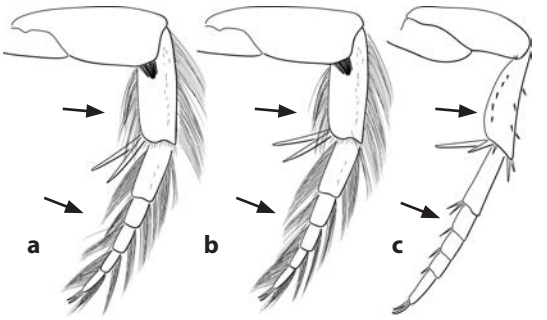


Fig. 7.2. Hydrotrupini left metalegs. **a**, *Platynectes decempunctatus* male. **b**, *P. decempunctatus* female. **c**, *Hydrotrupes palpalis*.

Key to the Genera of Hydrotrupini

1 Labial palpi short and broad, apical palpomere subquadrate (Fig. 7.3a); western North America and China (Map 7.3) . . . . . *Hydrotrupes*, 59

1' Labial palpi elongate and slender, apical palpomere elongate (Fig. 7.3b) 2

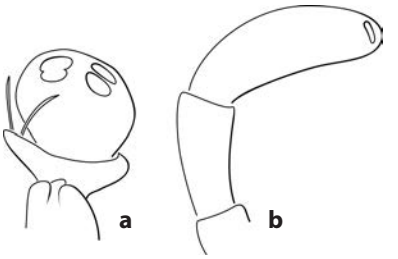


Fig. 7.3. Hydrotrupini labial palpi. **a**, *Hydrotrupes palpalis*. **b**, *Platynectes decempunctatus*.

2(1) Pronotum without lateral marginal bead (Fig. 7.4a). 3
2' Pronotum with lateral marginal bead (Fig. 7.4b). 4

3(2) Metacoxal lines absent or indistinct (Fig. 7.5a); Neotropical (Map 7.1) . . . . . .*Agametrus*, 58
3' Metacoxal lines present and distinct (as in Fig. 7.5b); Neotropical (Map 7.4). .*Leuronectes*, 60

4(2) Metacoxal lines present and distinct (Fig. 7.5b); Neotropical and Australasian (Map 7.5) . . . . . *Platynectes,* 60
4' Metacoxal lines absent or indistinct (as in Fig. 7.5a); Neotropical (Map 7.2). . *Andonectes*, 58

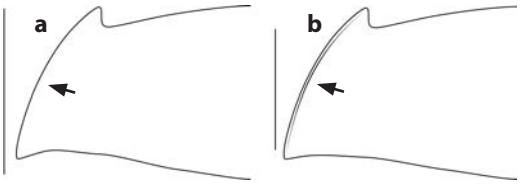


Fig. 7.4. Hydrotrupini pronota. **a**, *Agametrus humilis*. **b**, *Platynectes reticulosus*. Scales = 1.0mm.

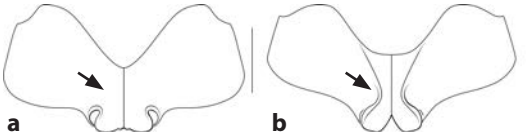


Fig. 7.5. Hydrotrupini metacoxae. **a**, *Agametrus humilis*. **b**, *Platynectes decempunctatus*. Scales = 1.0mm.

Fig. 7.6. *Agametrus humilis*. Scale = 1.0mm.

Genus *Agametrus* Sharp, 1882

Body Length. 6.0–8.0mm.

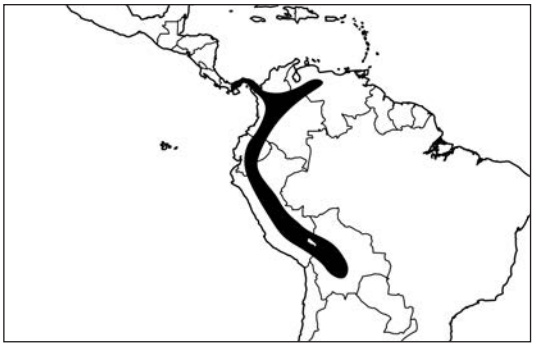
Diagnosis. *Agametrus* are Hydrotrupini with: (1) elongate palpomeres (as in Fig. 7.3b); (2) the pronotum without a lateral bead (Fig. 7.4a,6); and (3) the metacoxal lines absent (Fig. 7.5a). Members of the group are generally black, shiny, flattened, and moderately broad, though some have yellow maculae (Fig. 7.6).

Classification. Sharp (1882) considered *Agametrus* closely allied to *Leuronectes,* a conclusion also found by Ribera *et al*. (2008). *Agametrus* also appears to be nested within *Platynectes* (e.g., Ribera *et al*., 2008; Miller and Bergsten, 2014), and the genus will likely be synonymized in the near future based on a larger taxonomic sampling (Toussaint *et al.*, in press-a).

Diversity. This group includes seven species. They were revised by Guéorguiev (1971), but the group is poorly known taxonomically, and there are likely new species or possibly new synonyms.

Natural History. Specimens are found in springs and streams, often at high elevations.

Distribution. *Agametrus* are found in the high Andes from Bolivia north to Venezuela and into Central America in Panama (Map 7.1).



Map 7.1. Distribution of *Agametrus*.

Genus *Andonectes* Guéorguiev, 1971

Body Length. 5.9–10.7mm.

Diagnosis. *Andonectes* are Hydrotrupini with: (1) elongate palpomeres (as in Fig. 7.3b); (2) the pronotum with a lateral bead (as in Figs. 7.4b,7); and (3) the metacoxal lines absent (as in Fig. 7.5a). Members of the group are black, shiny, flattened, and moderately broad (Fig. 7.7).

Fig. 7.7. *Andonectes maximus*. Scale = 1.0mm. Photo by Patricia L. M. Torres and Mariano C. Michat. Used with permission.

Classification. This group was erected by Guéorguiev (1971) to single out the species *Platynectes aequatorius* Régimbart from all other *Platynectes* based on the absence of metacoxal lines. Like *Agametrus* and *Leuronectes*, it may well be found in the future that *Andonectes* is nested within *Platynectes*.

Diversity. There are now 14 species in this genus, the species *A. aequatorius* by Régimbart, a second, *A. maximus*, added by Trémouilles (2001), and 12 species by García (2002). Those by García (2002) are dubious given the numerous new species described, the very close proximity (or identity) of the type localities, and the minute differences used to diagnose them. A cursory examination of the types (Miller, unpublished) indicates they may, in fact, represent only one species, and are probably *Agametrus*. A revision of these taxa will be required to assess both the generic and specific status of species assigned to the group.

Natural History. Little is known of the natural history of *Andonectes*, but they are probably like *Platynectes* and *Agametrus* in being characteristic of streams, forest pools, and hygropetric habitats.

Distribution. Species are found in the northern Andes with one species found in the vicinity of São Paulo, Brazil (Map 7.2).

Map 7.2. Distribution of *Andonectes*.

Genus *Hydrotrupes* Sharp, 1882

Body Length. 4.0–4.7mm.

Diagnosis. The main character for this genus is the short and very robust maxillary and labial palpomeres, particularly the short and subquadrate apical labial palpomere (Fig. 7.3a). Natatory setae are absent on the legs (Fig. 7.2c). Other than this, there are few unique adult morphological features. Specimens are relatively small and black (Fig. 7.8).

Classification. See under Hydrotrupini for details regarding this genus and the history of the group with respect to its historical classification. The study by Miller and Bergsten (2014a) indicated that the genus is sister to all other Hydrotrupini.

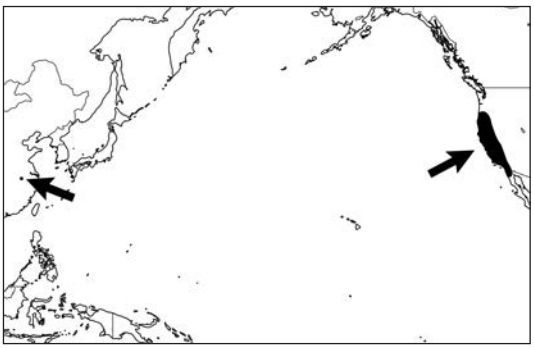
Diversity. The genus has two extant species, one known since Sharp's (1882) monograph, *H. palpalis* Sharp, the other described much more recently, *H. chinensis* Nilsson (2003b). *Hydrotrupes palpalis* was treated by Miller and Perkins (2012). Recently, a new species, *H. prometheus* Gómez and Damgaard, was described from Eocene Baltic amber (Gómez and Damgaard, 2014).

Natural History. *Hydrotrupes palpalis* are often hygropetric, living in films of water where it flows

Fig. 7.8. *Hydrotrupes palpalis*. Scale = 1.0mm.

over rocks or gathers in cracks in rock (Larson *et al.*, 2000). They have also been found to be "abundant in terrestrial shoreline habitats" (Hering, 1998). According to Hering (1998), specimens were found beneath the surface on sand bars more frequently than on gravel bars and were found with densities up to 25 individuals per square meter. They fed mainly on chironomid larvae (70% of prey items in the gut), but also preyed on other aquatic and subaquatic items (Hering, 1998). Despite the lack of swimming setae, specimens are apparently able to swim (Hering, 1998). The type series of *H. chinensis* was collected from a small pool in a nearly dry stream in a shaded gorge (Nilsson, 2003b). *Hydrotrupes* are able to jump very well using an unknown mechanism. Larvae were described by Alarie *et al.* (1998) and (in part) by Beutel (1994).

Distribution. This group has a dramatically disjunct distribution from the west coast of North America and east China (Map 7.3). Nilsson (2003b) discussed this interesting distribution in light of other water beetles with similar biogeographies. The discovery of *Hydrotrupes* in Baltic amber suggests the current disjunct distribution is a relict of a once more widespread, perhaps Holarctic, distribution (Gómez and Damgaard, 2014).



Map 7.3. Distribution of *Hydrotrupes*.

Genus *Leuronectes* Sharp, 1882

Body Length. 6.0–8.7mm.

Diagnosis. *Leuronectes* are Hydrotrupini with: (1) elongate palpomeres (as in Fig. 7.3b); (2) the pronotum without a lateral bead (as in Fig. 7.4a); and (3) the metacoxal lines present and distinctive (as in Fig. 7.5b). Members of the group are generally black, shiny, sometimes with small yellow maculae, flattened, and often somewhat more elongate than

Fig. 7.9. *Leuronectes curtulus*. Scale = 1.0mm.

Platynectes and *Agametrus* specimens (Fig. 7.9).

Classification. Little is known about *Leuronectes* classification or relationships. One sampled species from Peru was resolved as the sister to *Agametrus* in the phylogenetic study by Ribera *et al.* (2008). Each of these genera lacks a marginal bead laterally on the pronotum. Like *Agametrus*, *Leuronectes* was found nested among *Platynectes* species by Ribera *et al.* (2008) and will likely be synonymized in the near future based on a larger analysis (Toussaint *et al*., in press-a).

Diversity. There are five species in this genus that were revised by Guéorguiev (1971).

Natural History. Nothing much is known of the natural history of *Leuronectes*, though they are probably like *Platynectes* and *Agametrus* in being characteristic of streams and hygropetric habitats. They occur at high elevations in the Andes.

Distribution. *Leuronectes* is found in the Andes from central Chile and Argentina north to Colombia (Map 7.4).

Map 7.4. Distribution of *Leuronectes*.

Fig. 7.10. *Platynectes decempunctatus*. Scale = 1.0mm.

Genus *Platynectes* Régimbart, 1879

Body Length. 4.8–9.3mm.

Diagnosis. *Platynectes* are Hydrotrupini with: (1) elongate palpomeres (Fig. 7.3b); (2) the pronotum with a lateral bead (Fig. 7.4b); and (3) the metacoxal lines present and distinctive (Fig. 7.5b). Members of the group are mostly shiny, flattened, moderately broad and black, but often strikingly colored with yellow bands or maculae (Fig. 7.10). A couple of Australia species have longitudinal grooves or sulci on the elytra.

Classification. *Platynectes* has been variously divided into subgenera (Vazirani, 1970; 1976; Guéorguiev, 1972), which has produced some complicated nomenclatural problems (Vazirani, 1976). They are currently divided into three subgenera — *P*. (*Australonectes*) Guéorguiev, *P*. (*Gueorguievtes*) Vazirani, and *Platynectes s. str.* (Nilsson, 2001) — based mainly on the shape and nature of the metacoxal lines, though it is not clear at this time if the groups are monophyletic. The genus itself may be paraphyletic (Ribera *et al.*, 2008; Miller and Bergsten, 2014a).

Diversity. This is the largest genus in the tribe with 50 species. New World species were treated by Guéorguiev (1972). Old World species were treated by Vazirani (1970; 1976), Guéorguiev (1972), Watts (1978), Satô (1982), Hendrich and Balke (2000b), Brancucci (2008), and Brancucci and Vongsana (2010). The group is in need of comprehensive revision, and several new species are known from northern South America (Miller, unpublished).

Natural History. *Platynectes* are found in streams, seeps, and springs as well as small forest pools and hygropetric habitats. Some are widespread in various habitats, whereas others are very specific to particular habitats or localities.

Distribution. Members of the group have a disjunct distribution with most of the species found in Southeast Asia south throughout Australia and several species found in northeastern South America (Map 7.5). Toussaint *et al.* (in press-a) studied the biogeography of the genus and inferred an Eocene origin.

Map 7.5. Distribution of *Platynectes*.

8. Tribe Agabini

Body Length. 4.9–14.5mm.

Diagnosis. These are Agabinae with: (1) either linear, marginal foveae or linear grooves present at the anterolateral angles of the clypeus (Fig. 8.5b) or with a marginal groove across the entire clypeus (Fig. 8.5a), and (2) females without natatory setae along the ventral margins of the metatibia and metafemur (Fig. 8.1, except in the species, *Ilybius discedens*, which is derived within Agabini (Larson, 1987; Nilsson, 1996a; 2000)).

Classification. This group historically (as a tribe within Colymbetinae) included also the members of Hydrotrupini, though those taxa are evidently phylogenetically distinct from those placed here in Agabini (see below). Within Agabini, the genera have experienced some rearrangement over the past several years, particularly beginning with Nilsson (2000, as the *Agabus*-group of genera of Agabini). The main concern at that time was the genus *Agabus*, which was evidently paraphyletic. The name *Ilybiosoma* was resurrected to include certain species groups, and other *Agabus* were moved into *Platambus* and *Ilybius* (Nilsson, 2000). Later phylogenetic work largely corroborated this revised classification, though it now seems likely that both *Platambus* and *Agabus* remain paraphyletic and need further reclassification (Ribera *et al.*, 2004).

Diversity. Currently, there are six genera recognized in the tribe, including the genus *Hydronebrius*, which has been occasionally placed in its own tribe (e.g., Brinck, 1948).

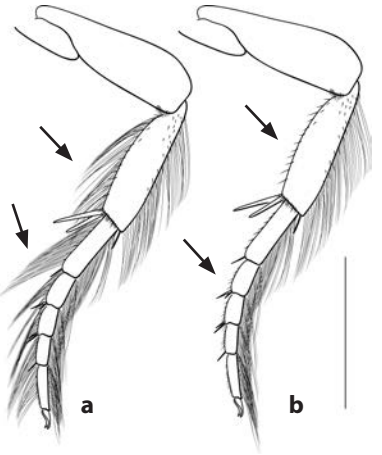


Fig. 8.1. *Agabus obliteratus* left metaleg. **a**, Male. **b**, Female. Scale = 1.0mm.

Natural History. This is a diverse group of diving beetles with members occurring in many habitats from permanent lentic and lotic waters to temporary vernal pools or rock pools, seeps and springs. There are species specializing in rheophilic situations and others in cold fens. Karyotype has been investigated in a few species in this group (Aradottir and Angus, 2004; Angus *et al.*, 2013).

Distribution. This is a largely Holarctic group with the greatest diversity across northern North America, Europe, and Siberia, with some species farther south in the Oriental region, into northern Central America and in high elevations of eastern Africa south into South Africa.

Key to the Genera of Agabini

1 Metacoxal lines parallel or subparallel to apex of metacoxal lobes (Fig. 8.2a); western Nearctic (Map 8.1) . . . . . *Agabinus*, 63

1' Metacoxal lines diverging onto metacoxal lobes and often anteriorly toward metasternum, narrowest part anterior of metacoxal processes (Fig. 8.2b) 2

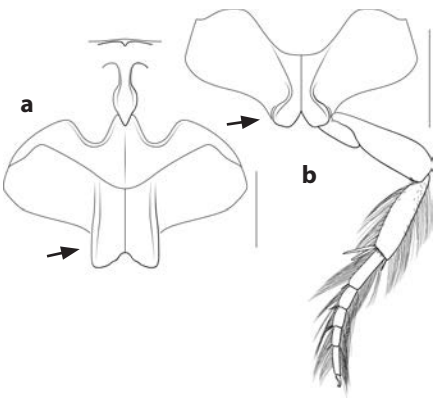


Fig. 8.2. Agabini ventral surfaces. **a**, *Agabinus glabrellus*, thoracic sternites. **b**, *Agabus obliteratus,* metacoxae and left metaleg. Scales = 1.0mm.

2(1) Prosternal process with lateral bead expanded posterior to procoxae (Fig. 8.3a); mesocoxae broadly separated; mainly Holarctic but also extending into Mexico and Oriental region (Map 8.6) . . . . . *Platambus*, 68

2' Prosternal process with lateral bead not expanded (Fig. 8.3b) 3

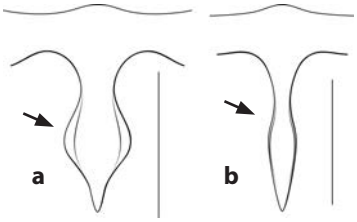


Fig. 8.3. Agabini prosternal processes. **a**, *Platambus maculatus*. **b**, *Agabus griseipennis*. Scales = 1.0mm.

3(2) Metafemur without linear series of closely placed setae near ventral margin of anteroapical angle of metafemur (Fig. 8.4a), metafemur with strong, conspicuous punctation (Fig. 8.4a); mountains of southern east Palearctic (Map 8.3) . . . . . *Hydronebrius*, 65

3' Metafemur with linear series of closely placed setae near ventral margin of anteroapical angle of metafemur (Fig. 8.4b), metafemur without strong, conspicuous punctation (Fig. 8.4b) . . 4

4(3) Anterior clypeal margin with bead (marginal groove) continuous (Fig. 8.5a); Holarctic south into Central America and the mountains of eastern Africa to South Africa (Map 8.2) . . . . . *Agabus* 64

4' Anterior clypeal margin with bead broadly interrupted medially, with only linear marginal grooves anterolaterally (Fig. 8.5b) 5

5(4) Pronotum with anterior marginal line continuous (Fig. 8.6a); Holarctic (Map 8.5) . . . . . *Ilybius*, 67

5' Pronotum with anterior marginal line interrupted medially (Fig. 8.6b); Nearctic south into Mexico and in isolated localities in northeastern Africa, the Middle East, and southern China (Map 8.4) . . . . . *Ilybiosoma*, 66

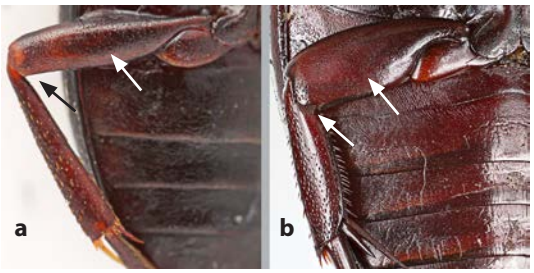


Fig. 8.4. Agabini right metaleg. **a**, *Hydronebrius cordaticollis*. **b**, *Ilybius ater*.

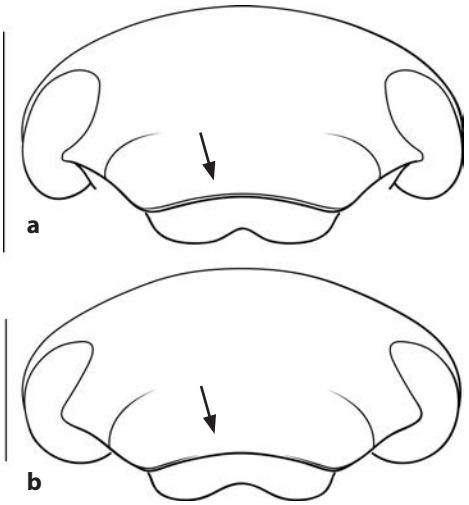


Fig. 8.5. Agabini heads, anterior aspect. **a**, *Agabus obliteratus*. **b**, *Ilybiosoma lugens*. Scales = 1.0mm.

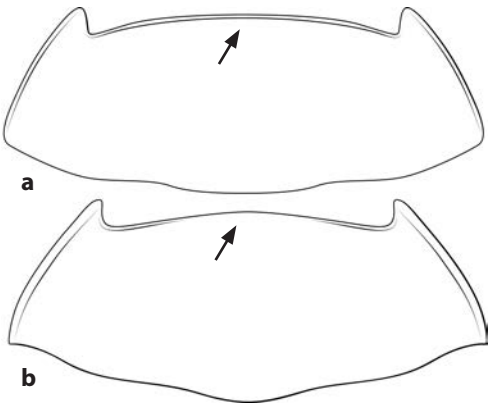


Fig. 8.6. Agabini pronota. **a**, *Ilybius ater*. **b**, *Ilybiosoma lugens*. Scales = 1.0mm.

Genus *Agabinus* Crotch, 1873

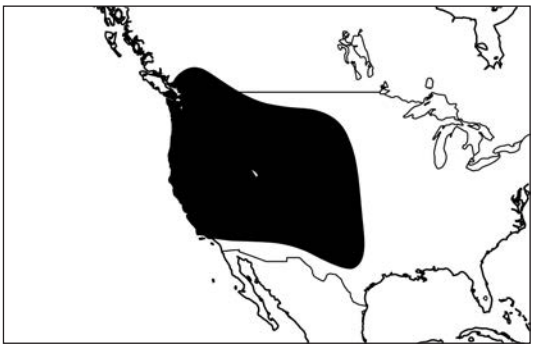
Body Length. 4.9–6.7mm.

Diagnosis. These are Agabini distinguished by: (1) strongly impressed and parallel metacoxal lines, not divergent anteriorly toward metasternum nor posteriorly toward metacoxal processes (Fig. 8.2a); (2) with the lateral bead of the prosternal process expanded posterior to the procoxae (Fig. 8.2a); (3) the mesocoxae relatively broadly separated (Fig. 8.2a); and (4) natatory setae absent from the ventral margins of the metatibia and metatarsus in both sexes (as in Fig. 8.1b). Members of this group are relatively small, broadly oval in outline, and black (Fig. 8.7).

Fig. 8.7. *Agabinus glabrellus*. Scale = 1.0mm.

Classification. *Agabinus* was recognized as a separate genus, distinguished by the shape of the metacoxa, since Crotch (1873) and Sharp (1882), until reclassification by Nilsson (2000) resulted in the expansion of *Platambus* to include this genus. Nilsson (2000) noted that *Agabinus* shared with *Platambus* the posteriorly expanded lateral beads of the prosternal process, a historically important synapomorphy for the latter genus. This relationship was partly supported in the analysis by Ribera *et al.* (2004), but *Agabinus* exhibited unusually long branches and was difficult to place among the Agabini groups. Although fewer Agabini taxa were sampled, that phylogenetic position was not supported in the analysis by Ribera *et al.* (2008), and *Agabinus* was instead resolved as sister group to the *Agabus*-group of genera. Alarie and Larson (1998) described the larvae of *A. glabrellus* (Motschulsky), and, based on larval characters, postulated a sistergroup relationship between *Agabinus* and the clade *Hydrotrupes* + *Agabus* + *Ilybius*. Nilsson (2015) subsequently resurrected the genus, a classification that we follow here.

Diversity. There are two species in this genus, *A. glabrellus* (Motschulsky) and *A. sculpturellus* Zimmermann, that can be identified with the key presented by Larson *et al.* (2000).



Map 8.1. Distribution of *Agabinus*.

Natural History. The two species are mainly found in mountain streams and springs. Alarie and Larson (1998) speculated that the unusual metacoxal and metathoracic leg morphology could be an adaptation to living interstitially or under cover.

Distribution. This genus is restricted to the western Nearctic from British Columbia to California eastward to South Dakota and Texas (Map 8.1).

Genus *Agabus* Leach, 1817

Body Length. 5.1–13.5mm.

Diagnosis. Within Agabini this group is characterized by the following: (1) with a distinct linear series of closely placed setae near the ventral margin of the anteroapical angle of the metafemur (as in Fig. 8.4b); (2) the anterior clypeal margin with the bead (marginal groove) continuous (Fig. 8.5a); and (3) the prosternal process with the lateral bead not expanded posterior to the procoxae (Fig. 8.3b). Many species are testaceous or black (Fig. 8.8a,c), but others are conspicuously maculate or colorful (Fig. 8.8b).

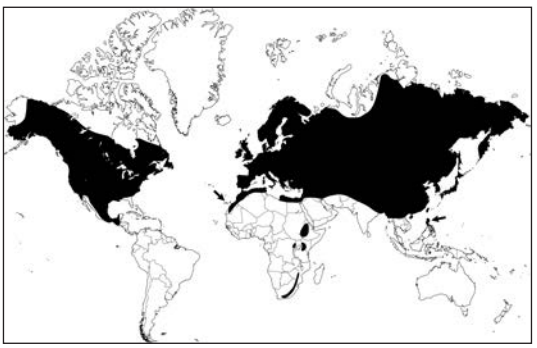
Classification. Historically, *Agabus* included species that are now placed in *Platambus*, *Ilybius,* and *Ilybiosoma* until reclassification of the tribe by Nilsson (2000). He also classified the group into three subgenera — *A*. (*Acatodes*), *A*. (*Gaurodytes*), and *Agabus s. str.* — provided a key for their identification, and further organized the species into species groups. The subgenera differ primarily in characteristics of the male genitalia and a few other subtle and indistinct features that can be difficult to assess. Even with this restructuring, however, *Agabus* appears to be paraphyletic with respect to certain groups of *Platambus* (Ribera *et al.*, 2004).

Diversity. As currently defined, this is a large group with 172 species. The Nearctic taxa have been revised in a series of papers (Larson and Nilsson, 1985; Larson, 1989; 1991b; 1994; 1996b; 1997b; Larson and Wolfe, 1998) with keys to all species in Larson *et al.* (2000). Palearctic and Afrotropical species can be identified using various sources (Nilsson, 1990; 1992a; b; 1994b; c; 2003a; Nilsson and Larson, 1990; Millán and Ribera, 2001). Species are often extremely similar and difficult to identify with the main diagnostic features associated with the

Fig. 8.8. *Agabus* species. **a**, *A. canadensis*. **b**, *A. disintegratus*. **c**, *A. tristis*. Scales = 1.0mm.

male genitalia.

Natural History. Most members of this group are in shallow lentic habitats, including temporary situations such as vernal snowmelt pools. Others are principally lotic, occurring along stream margins or in springs. At about 5,100m elevation, members of *Agabus* are among the highest occurring diving beetles (Brancucci and Hendrich, 2008). Much has been written about their natural history, especially in Europe (Galewski, 1976a; c; Carr and Nilsson, 1988; Nilsson and Soderstrom, 1988; Carr, 1990; Barman *et al.*, 1999; 2000; Brannen *et al.*, 2005; Culler and Lamp, 2009). Recent work has been done on the compound eye morphology of *A. japonicus* Sharp (Jia and Liang, 2014). Larvae of many species have been described (Galewski, 1963b; 1968a; 1972a; b; 1973a; 1974b; c; 1976a–d; 1978b–d; 1979a–c; 1980; 1981b–c; 1982a–c; 1983a,b; 1984a–d; 1986a–e; 1987b; de Marzo, 1973; 1974b; Hilsenhoff, 1974; Nilsson, 1979; 1980; 1982a–d; 1983a; b; 1984a; b; 1987a; 1988; 1992a; Nilsson and Cuppen, 1983; Cuppen and Dettner, 1986; Matta, 1986; Carr and Nilsson, 1988; Carr, 1990; Dettner *et al.*, 1995; Barman *et al.*, 1999; 2000).



Map 8.2. Distribution of *Agabus*.

Distribution. This is a primarily Holarctic group with a few species extending south into Mexico and Central America, the Philippines, and south into high-elevation areas of Africa (Map 8.2).

Genus *Hydronebrius* Jakovlev, 1897

Body Length. 7.9–10mm.

Diagnosis. *Hydronebrius* are medium-sized agabines with coarsely and densely punctate metafemora (and other ventral surfaces) and without a distinct linear series of closely placed setae near the ventral margin of the anteroapical angle (Fig. 8.4a). The pronotum is cordate (Fig. 8.9).

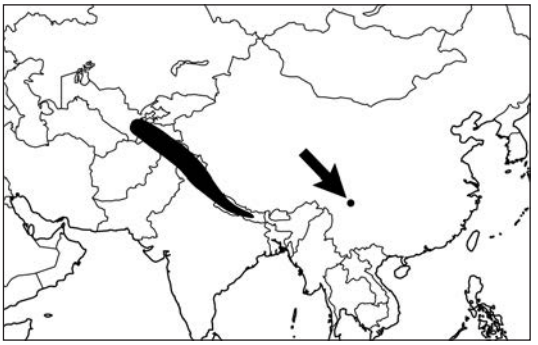
Fig. 8.9. *Hydronebrius cordaticollis*. Scale = 1.0mm.

Classification. The group has been placed as a genus in its own tribe (Brinck, 1948; Guignot, 1948b), but also as a subgenus of *Gaurodytes* (now a subgenus of *Agabus*) (e.g., Zaitzev, 1953). One species was actually originally placed in Amphizoidae (Vazirani, 1964a).

Diversity. There are currently four species and one subspecies in this obscure group. They have had only sporadic taxonomic treatment (Brancucci, 1980a; Kavanaugh and Roughley, 1981; Toledo, 1993).

Natural History. *Hydronebrius* occur in the margins of mountain torrents (Brancucci, 1980a).

Distribution. Species are found in central Asia (Map 8.3).



Map 8.3. Distribution of *Hydronebrius*.

Genus *Ilybiosoma* Crotch, 1873

Body Length. 6.9–13.2mm.

Map 8.4. Distribution of *Ilybiosoma*.

Diagnosis. *Ilybiosoma* are characterized by the following: (1) the anterior clypeal marginal bead is discontinuous medially (medially effaced) (Fig. 8.5b); (2) the lateral bead of the prosternal process is not expanded posterior to the procoxae (as in Fig. 8.3b); (3) the mesocoxae are relatively narrowly separated; and (4) the pronotum has the anterior marginal line distinctly interrupted medially (Fig. 8.6b). Many are relatively robust Agabinae, and most are dark colored (Fig. 8.10). Some have the pronotum distinctly cordate (Fig. 8.10b).

Classification. As currently classified, this group includes representatives historically placed in *Agabus* until the reclassification by Nilsson (2000). The group was demonstrably monophyletic in the analysis by Ribera *et al.* (2004), though relationships of the genus to others in Agabini remain ambiguous.

Diversity. The genus currently includes 17 species. Most of the species are Nearctic and can be identified using a revision by Larson (1997b) and Larson *et al.* (2000). The one African species was treated by Nilsson (1992b), the one Iranian species by J. Balfour-Browne (1939a), and the one Tibetan spe-

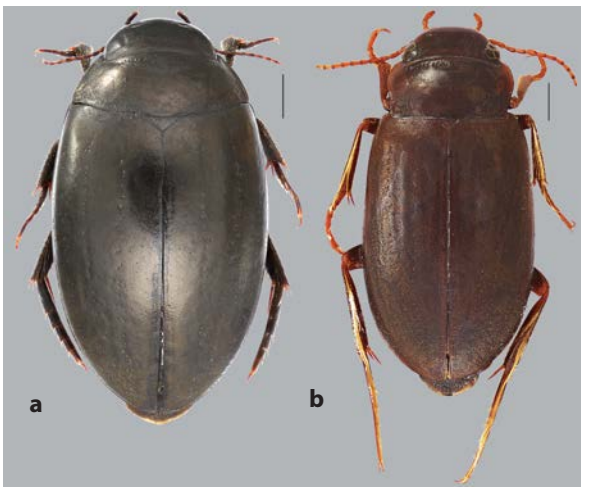


Fig. 8.10. *Ilybiosoma* species. **a**, *I. lugens*. **b**, *I. cordatum*. Scales = 1.0mm.

cies by Brancucci and Hendrich (2006).

Natural History. These species are found in a lotic habitats from seeps and springs to margins of larger streams (Larson and Wolfe, 1998).

Distribution. *Ilybiosoma* are mainly found in the western Nearctic with one species extending in the eastern Nearctic and a few species endemic to small regions in Ethiopia, Iran, and Tibet (Map 8.4).

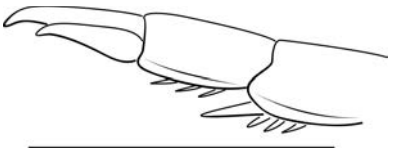
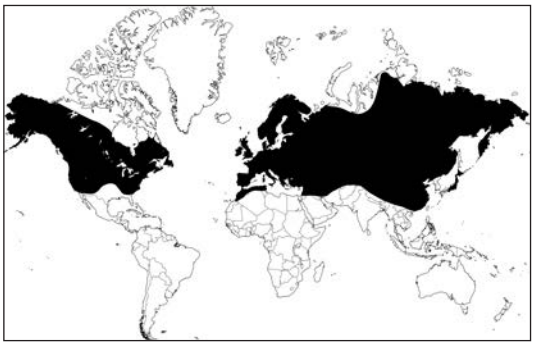


Fig. 8.11. *Ilybius picipes*, metatarsomeres and metatarsal claws. Scale = 1.0mm.

Genus *Ilybius* Erichson, 1832

Body Length. 5.3–14.5mm.

Diagnosis. *Ilybius* is characterized within Agabini by the following: (1) the anterior clypeal margin with the bead discontinuous medially (as in Fig. 8.5b); (2) the prosternal process with the lateral bead not expanded posterior to the procoxae (as in Fig. 8.3b); (3) the mesocoxae relatively narrowly separated; and (4) the pronotum with the anterior marginal line continuous medially (Fig. 8.6a). Many members of *Ilybius* (the *I. subaeneus* group) have the metatarsal claws distinctly unequal (Fig. 8.11). Species range from relatively small to fairly large in size, and most members of the group vary from testaceous to black



Map 8.5. Distribution of *Ilybius*.

(Fig. 8.12) though some are maculate.

Classification. Historically, *Ilybius* included a smaller group of taxa characterized by unequal metatarsal claws and endophytic oviposition with a knife-like ovipositor (the *I. subaeneus* group, Wallis, 1939a; Larson, 1987; Nilsson, 1994b; Miller, 2001c). After the reclassification by Nilsson (2000), the genus was expanded to include numerous species previously placed in *Agabus*.

Diversity. There are currently 71 species in this large group. North American species can be identified using revisionary work by Larson (1987; 1996b) and Larson *et al.* (2000). Palearctic species can be identified using works by Zimmermann (1934), Zimmermann and Gschwendtner (1935), Zaitsev and Pavlovski (1972), Fery and Nilsson (1993), and Nilsson and Holmen (1995).

Natural History. These species occur in many habitats from boreal or high-elevation bogs and lake margins to seeps and stream margins, usually in areas with considerable vegetation. Many members oviposite endophytically (Jackson, 1960b; Miller, 2001c). Several scientists have investigated *Ilybius*

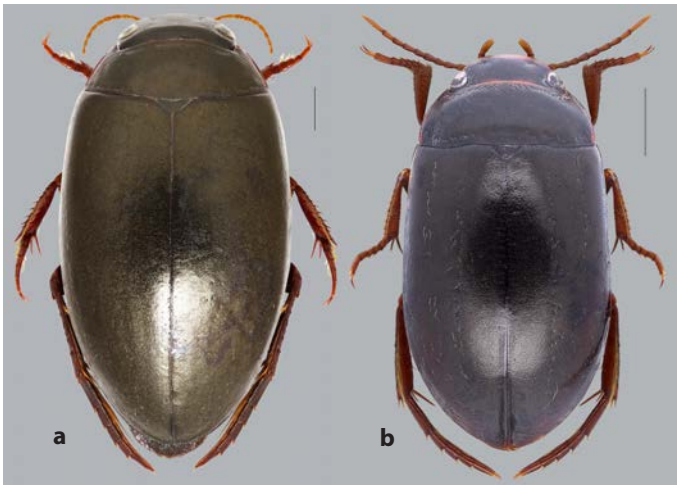


Fig. 8.12. *Ilybius* species. **a**, *I. fraterculus*. **b**, *I. wasastjernae*. Scales = 1.0mm.

Fig. 8.13. *Platambus* species. **a**, *P. maculatus*. **b**, *P. semivittatus*. Scales = 1.0mm.

biology and life history (Jackson, 1960b; Nilsson, 1986c; Hicks and Larson, 1991; 1995; Barman *et al.*, 2001; Dolmen and Solem, 2002a). Others have investigated food habits (Hicks, 1994; Bosi, 2001). Still others have investigated dispersal, colonization, and movement patterns (Denton, 1997; Davy-Bowker, 2002; Dolmen and Solem, 2002b). Several larvae have been described (Galewski, 1966; 1987b; Nilsson, 1981; Nilsson and Kholin, 1997; Hicks and Larson, 2000).

Distribution. This group is Holarctic with representatives in the far north, south to the northern coast of Africa in the Palearctic, and south to Mexico in the Nearctic (Map 8.5). Some species have Holarctic distributions.

Genus *Platambus* Thomson, 1859

Body Length. 5.1–12.5mm.

Diagnosis. These are small- to medium-sized diving beetles with (as in Fig. 8.4b) or (more rarely) without (as in Fig. 8.4a) a distinct linear series of closely placed setae near ventral margin of the anteroapical angle of the metafemur, with the lateral bead of the prosternal process generally expanded posterior to the procoxae (Fig. 8.3a) and the mesocoxae broadly separated. Members of *Platambus* are typically oval and black or reddish-black, often with distinct maculae (Fig. 8.13).

Classification. As with other genera in the tribe, *Platambus* underwent a reclassification by Nilsson (2000), resulting in the expansion of *Platambus* to include several groups previously placed in *Agabus*. However, the group as so defined appears to not be monophyletic (Ribera *et al.*, 2004).

Diversity. *Platambus* currently includes 66 species. The Palearctic species were treated by Brancucci (1982a; b; 1984; 1988; 1990; 1995) and Vazirani (1965). Nearctic species were historically placed in several species groups of *Agabus* until reclassified by Nilsson (2000). They can be identified using keys by Leech (1941a), Larson and Wolfe (1998), and Larson *et al.* (2000).

Natural History. This diverse group occurs in a range of habitats, but especially lotic areas in marginal vegetation. Members also occur in small ponds and ditches.

Distribution. This is a Holarctic group with representatives extending into Southeast Asia and Mexico (Map 8.6).

Map 8.6. Distribution of *Platambus*.

9. Subfamily Colymbetinae

Body Length. 5.7–23.0mm.

Diagnosis. These are Dytiscidae with: (1) the eyes anteriorly emarginate (Fig. 9.1a); (2) the male median lobe bilaterally asymmetrical but not generally strongly so; (3) the lateral lobes bilaterally symmetrical; (4) the female gonocoxae flattened and apically rounded (Fig. 9.1b); (5) the prosternum and prosternal process together in the same plane (see Fig. 2.10b); and (6) the apices of the elytra evenly rounded (e.g., Fig. 9.12). Most taxa in this subfamily also have the metatarsal claws unequal (e.g. Fig. 9.3), and abdominal pleurite II with distinct transverse rugae (Fig. 9.2, not visible with the elytra closed).

Classification. The subfamilies Agabinae, Matinae, Copelatinae, Coptotominae, and Lancetinae, and the tribe Agabetini (Laccophilinae), were, for much of dytiscid taxonomic history, placed in this subfamily. This changed as the classification began to more adequately reflect phylogenetic history and it became clear that older ideas about the subfamily are not natural (e.g., Burmeister, 1976; de Marzo, 1976c; Ruhnau and Brancucci, 1984; Ruhnau, 1986; Burmeister, 1990; Beutel, 1994; 1998; Larson *et al.*, 2000; Miller, 2001c). The composition of the subfamily was mostly restricted to its current delimitation by Miller (2001c). Brinck (1948) placed the two Oceanic island species, *Rhantus tristanicola* (Brinck) and *Rhantus selkirki* Jäch, Balke & Michat (at that time in the genera *Senilites* and *Anisomeria*) together in their own tribe, Anisomeriini Brinck, based especially on their equal metatarsal claws. Recent analysis by Morinière *et al.* (2014) revealed that these two genera are actually nested well within the genus *Rhantus*, and they were synonymized. As a whole, Colymbetinae is evidently sister group to Agabinae (Miller and Bergsten, 2014a).

Diversity. Colymbetinae includes eight genera.

Natural History. Members of this group occur in a very wide variety of habitats from the Arctic to low-

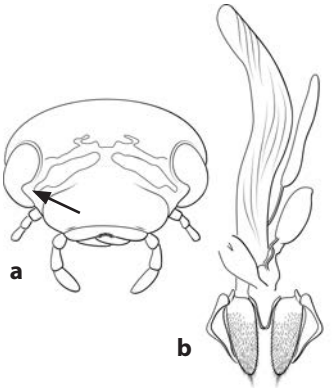


Fig. 9.1. Colymbetinae features. **a**, *Colymbetes exaratus* head, anterior aspect. **b**, *Rhantus binotatus* female reproductive tract, ventral aspect.

land tropical streams and ponds. The group includes some of the most northerly occurring Dytiscidae, including *Colymbetes dolabratus* (Paykull), which is found in Greenland in pools near glaciers. *Rhantus* are often exceptional dispersers, and some are found on extremely remote islands, including Hawaii and the Galápagos. Some are characteristic of boreal peat bogs, others are found in high-elevation clear pools, and others, such as *Meladema*, are found in large streams. These are often big beetles and significant predators where they occur.

Distribution. Colymbetines are found worldwide from the Arctic to extreme southern localities and on many remote islands. The greatest generic diversity is in the Holarctic region, with most austral members of the group in the genus *Rhantus*.

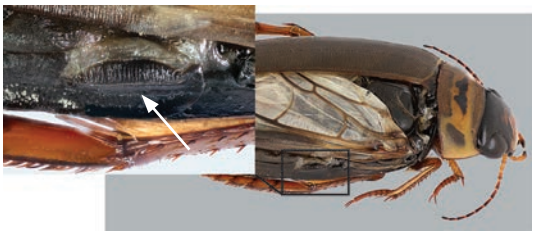


Fig. 9.2. *Colymbetes exaratus* pleurite II.

Key to the Genera of Colymbetinae

1 Metatarsomeres I–IV with apical margins straight, not lobed (Fig. 9.3a); New Guinea (Map 9.2). . . . . *Carabdytes*, 72

1' Metatarsomeres I–II or I–IV with apical margins curved or sinuate, with distinct apical lobes (Fig. 9.3b). 2

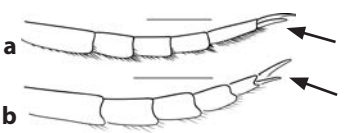


Fig. 9.3. Colymbetinae metatarsus. **a**, *Carabdytes upin*. **b**, *Rhantus suturalis*. Scales = 1.0mm.

2(1) Body dorsoventrally compressed (Fig. 9.15); prosternal process medially flattened (Fig. 9.4); pronotal marginal bead broad (Fig. 9.15); eastern North America (Map 9.4) . . . *Hoperius*, 73

2' Body not dorsoventrally compressed; prosternal process medially rounded to carinate; pronotal marginal bead absent (Fig. 9.5a) or more narrow (Fig. 9.5b) 3

3(2) Pronotum without lateral bead (Fig. 9.5a). . . 4

3' Pronotum with lateral bead (Fig. 9.5b) 8

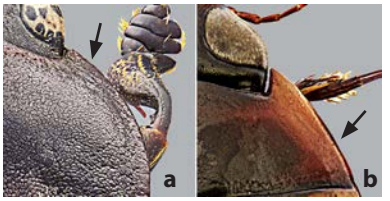


Fig. 9.5. Colymbetinae, right pronotal margin. **a**, *Neoscutopterus angustus*. **b**, *Rhantus calidus*.

4(3) Metatarsal claws subequal in length (Fig. 9.6a); pronotum narrowed posteriorly to base, outline discontinuous (Fig. 9.7a). 5

4' Metatarsal claws distinctly unequal in length (Fig. 9.6b); pronotum widest at base, outline continuous (Fig. 9.7b) 6

Fig. 9.6. Colymbetinae, metatarsal claws. **a**, *Rhantus selkirki*. **b**, *Rhantus suturalis*.

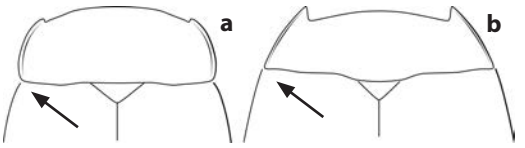


Fig. 9.7. Colymbetinae dorsal surfaces. **a**, *Bunites distigma*. **b**, *Rhantus calidus*.

5(4) Size larger (length > 13mm); high Andes of South America (Map 9.1) . . . . . *Bunites*, 71

5' Size smaller (length < 12mm), Tristan da Cuhna and Juan Fernandez . . *Rhantus* (in part), 76

6(4) Elytral sculpturing composed of large, irregular, prominently incised cells (Fig. 9.8a); protibia emarginate along ventral margin near base, more pronounced in males (Fig. 9.9a); northern Nearctic region (Map 9.7) . . . . . *Neoscutopterus*, 75

6' Elytral sculpturing not composed of large, irregular, prominently incised cells; protibia not or weakly emarginate along ventral margin near base (e.g., Fig. 9.9b) 7

Fig. 9.4. *Hoperius planatus*, prosternum and prosternal process.

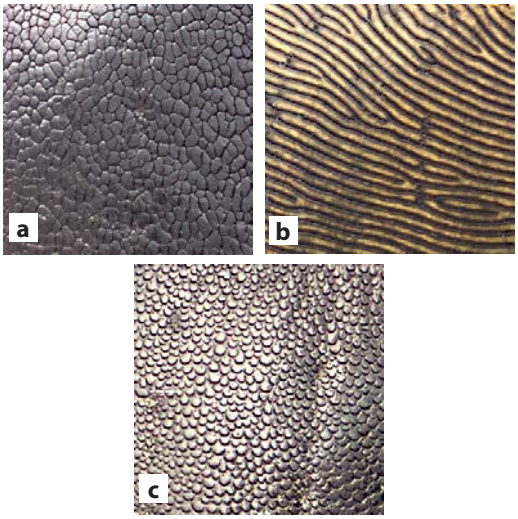


Fig. 9.8. Colymbetinae, elytral surface sculpture. **a**, *Neoscutopterus angustus*. **b**, *Colymbetes exaratus*. **c**, *Meladema coriacea*.

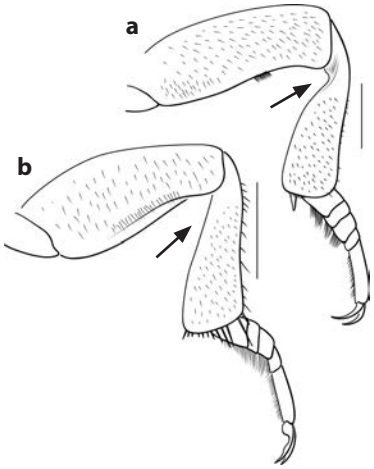


Fig. 9.9. Colymbetinae, proleg. **a**, *Neoscutopterus angustus*. **b**, *Colymbetes fuscus*. Scales = 1.0mm.

7(6) Anterior margin of metaventrite weakly incised for reception of prosternal process (Fig. 9.10a); elytral sculpturing in most species composed of dense, transverse, parallel grooves (Fig. 9.8b); Holarctic (Map 9.3) . . . . . *Colymbetes*, 72

7' Anterior margin of metaventrite deeply incised for reception of prosternal process (Fig. 9.10b); elytral sculpturing composed of short, curved striae making scale-like sculptures (Fig. 9.8c); southern Europe and northwestern Africa, Madeira, Canaries (Map 9.5) . . . . . *Meladema*, 74

8(3) Anterior surface of metatibia covered with setigerous punctures (Fig. 9.11a); southern Europe (Map 9.6) . . . . . *Melanodytes*, 74

8' Anterior surface of metatibia with few setigerous punctures in distinct linear series (Fig. 9.11b); worldwide (Map 9.8) . . . . . *Rhantus* (in part), 76

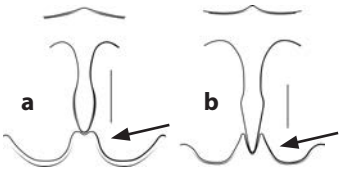


Fig. 9.10. Colymbetinae prosternal processes and anterior margin of metaventrite. **a**, *Colymbetes fuscus*. **b**, *Meladema coriacea*. Scales = 1.0mm.

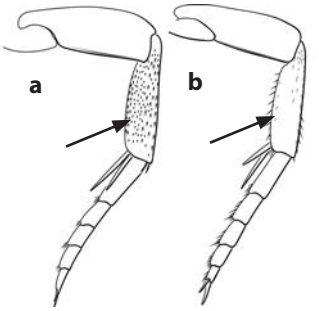


Fig. 9.11. Colymbetinae left metaleg. **a**, *Melanodytes pustulatus*. **b**, *Rhantus sinuatus*.

Fig. 9.12. *Bunites distigma*. Scale = 1.0mm.

Genus *Bunites* Spangler, 1972

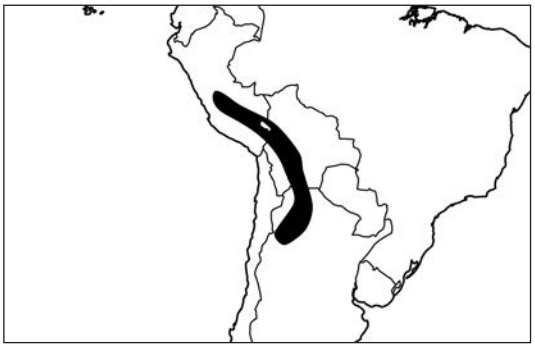
Body Length. 14.0–14.5mm.

Diagnosis. The single species in this genus is characterized by: (1) the lateral outline distinctly discontinous between the pronotum and elytron (Figs. 9.7a,12); (2) the anteromedial margin of the metaventrite deeply impressed for reception of the prosternal process (as in Fig. 9.10b); (3) the pronotum with a distinct lateral bead (Figs. 9.7a,12); (4) metatarsomeres I–II moderately lobed on the anteroventral apex; and (5) the metatarsal claws subequal in length (as in Fig. 9.6a). Specimens are large, elongate, and dorsally darkened with lateral maculae on the elytra (Fig. 9.12).

Classification. Details about *Bunites* classification were discussed by Spangler (1972), Bachmann and Trémouilles (1982), and Trémouilles and Bachmann (1989). Based on first-instar larval characters the genus was reported as most closely related to *Meladema* and *Neoscutopterus* (Michat, 2005), but this was not supported by molecular data, which instead clearly indicated affinities with the genus *Rhantus* (Morinière *et al.*, 2014).

Diversity. There is a single species in this genus, *B. distigma* (Brullé).

Natural History. The single poorly known species has been collected at high elevation in a puna grassland pool (Spangler, 1972). The larvae were described by Michat (2005) based on material collected from a pond with some vegetation at an eleva-



Map 9.1. Distribution of *Bunites*.

tion of around 2,000m in Argentina. Michat (2005) reported that adults were also collected from a nearby shaded stream.

Distribution. This species is known only from Bolivia and Argentina north into Peru (Map 9.1).

Genus *Carabdytes* Balke, Hendrich and Wewalka, 1992

Body Length. 11.2–13.4mm.

Diagnosis. The single species in the genus is very "caraboid" and has a distinctly cordate pronotum and long legs (Fig. 9.13). Also, metatarsomeres I–IV have the apical margin straight (Fig. 9.3a), whereas members of the rest of the tribe have some of the metatarsomeres with the apical margin sinuate, with a distinct lobe (Fig. 9.3b). The transverse rugae on the pleuron of abdominal segment II (e.g., Fig. 9.2) are only weakly developed (not visible with the elytra closed).

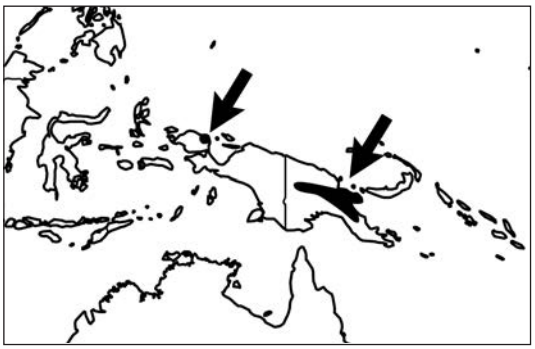
Classification. Relationships between *Carabdytes* and other Colymbetinae have been controversial. The single species was placed in its own tribe, Carabdytini Pederzani (1995), which was synonymized with Colymbetini by Nilsson and Roughley (1997), re-elevated by Miller (2001c), but questioned by Balke (2001a) and Balke *et al.* (2007a), and finally again synonymized with Colymbetini by Morinière *et al.* (2014). *Carabdytes* seem to be nested within a clade of New Caledonian and Pacific colymbetine species currently classified as *Rhantus* (Balke *et al.*, 2007a; 2009), but a reclassification, potentially transferring a number of *Rhantus* species to *Carabdytes* (Skale *et al.*, 2012), is awaiting a more thoroughgoing investigation including many of the diverse groups within *Rhantus* (Balke *et al.*, 2007a; in prep.).

Fig. 9.13. *Carabdytes upin*. Scale = 1.0mm.

Diversity. There is a single species — *Carabdytes upin* Balke, Hendrich and Wewalka — with two subspecies (Skale *et al.*, 2012).

Natural History. *Carabdytes* live in shaded streams and cold, fast-flowing, mountain rivers, where they live under and between stones and in high-altitude *Sphagnum* pools on peat (Skale *et al.*, 2012). Biogeography of the two recognized subspecies was investigated by Skale *et al.* (2012). The larva was described by Alarie and Balke (1999).

Distribution. The single species in this genus is found in New Guinea (Map 9.2).



Map 9.2. Distribution of *Carabdytes*.

Genus *Colymbetes* Clairville, 1806

Body Length. 9.0–20.0mm.

Diagnosis. Most *Colymbetes* are easily recognized by the elytron covered with closely spaced, transverse, subparallel grooves (Figs. 9.8b,14). *Colymbetes minimus* Zaitzev does not have these grooves; instead there are only a few transverse series of punctures, and *C. piceus* Klug is variable with some specimens with the grooves and others without them (Zaitzev, 1953; Zimmerman, 1981). However, all specimens are characterized by: (1) the anterior medial margin of the metaventrite not emarginate for reception of the prosternal process (Fig. 9.10a); (2) no lateral bead on the pronotum (Fig. 9.14); (3) the metatarsal claws distinctly unequal in length; and (4) male protarsomeres I–III ventrally with dense adhesive setae, distinct, elongate oval adhesive discs, or both (see Fig. 2.11h). These beetles are relatively large and yellow or light brown to black (Fig. 9.14).

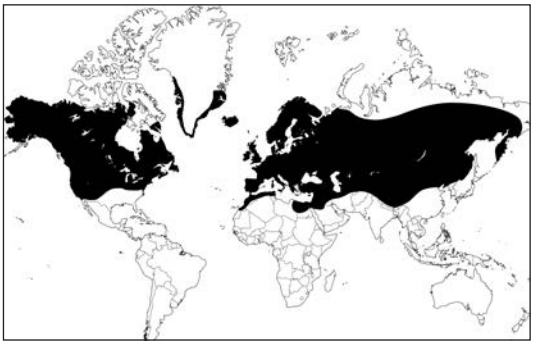
Fig. 9.14. *Colymbetes exaratus*. Scale = 1.0mm.

Classification. *Colymbetes* is distinctive within the family and has long had its current definition. European workers have recognized two subgenera, *Colymbetes s. str.* and *C.* (*Cymatopterus*) Dejean based on the nature of the ventral adhesive setae on male protarsomeres I–III (*Colymbetes s. str.* with adhesive discs, *C.* (*Cymatopterus*) with adhesive setae but without discs). However, the monophyly of these two groups has not been adequately tested, and the ventral adhesive structures on the male protarsomere are intermediate in certain North American taxa. Many workers have not recognized this classification (e.g., Larson, 1975; Nilsson, 2015).

Diversity. There are currently 22 species and 2 subspecies in the genus. The North American species were revised first by LeConte (1862), but more recently by Zimmerman (1981) with modifications to his classification by Larson *et al.* (2000) and Drotz *et al.* (2015). Palearctic species have been treated by Nilsson and Holmen (1995), Nilsson (2002), Dettner (1983), and Balke (2003).

Natural History. These beetles are found in various lentic habitats from bogs and fens to prairie pools. Some species, particularly *C. paykulli* Erichson, are characteristic of cold *Sphagnum* bogs. *Colymbetes dolabratus* (Paykull) survives in cold, coastal subarctic pools. Studies of water current detection and swimming in *C. fuscus* (Linnaeus) were conducted by Gewecke (1996), and defensive chemistry of *C. fuscus* was investigated by Schildknecht and Tacheci (1971). Larvae of several species have been described (Galewski, 1964; 1967; 1968b; 1990a; Nilsson and Cuppen, 1988).

Distribution. This is a Holarctic group with at least two nominal species occurring in both the Nearctic and Palearctic regions (Map 9.3) (e.g., Drotz *et al.*, in prep.). This group includes one of the most northerly occurring of any diving beetle, *C. dolabratus*, in Greenland (Map 9.3).



Map 9.3. Distribution of *Colymbetes*.

Genus *Hoperius* Fall, 1927

Body Length. 12.0–14.0mm.

Diagnosis. *Hoperius* are characterized by the following combination: (1) the body depressed with the dorsal surface flat (Fig. 9.15) and prosternal process flat (Fig. 9.4); (2) the lateral margins of the pronotum with a broad bead (Fig. 9.15); and (3) the elytra with coarse reticulation (Fig. 9.15).

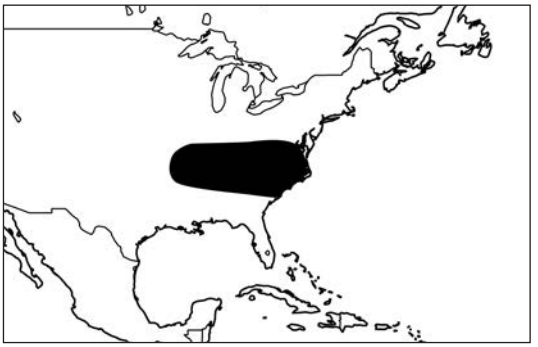
Classification. Within Colymbetinae, *Hoperius* seem to be most closely related to the other Nearctic genus *Neoscutopterus* (Ribera *et al.*, 2008; Miller and Bergsten, 2014a; Morinière *et al.*, 2014).

Diversity. There is only a single, uncommon species in this genus, *H. planatus* Fall. Spangler (1973a) reviewed the species.

Fig. 9.15. *Hoperius planatus*. Scale = 1.0mm.

Natural History. *Hoperius planatus* occurs mainly in woodland pools with considerable leaf pack (Spangler, 1973a). Spangler (1973a) provided details on the natural history of the species and described the larva. Larvae were redescribed by Alarie and Hughes (2006) and Barman *et al.* (2006; 2014).

Distribution. The species is found in eastern North America from Arkansas east to Maryland and South Carolina (Map 9.4).



Map 9.4. Distribution of *Hoperius*.

Genus *Meladema* Laporte, 1835

Body Length. 20.0–23.0mm.

Diagnosis. *Meladema* are large, black, or testaceous beetles (Fig. 9.16) with the following combination within Colymbetinae: (1) the pronotum lacks a lateral bead (Fig. 9.16); (2) the elytral sculpturing is composed of short, curved striae that form scale-like structures (Fig. 9.8c); (3) the protibia is only slightly emarginate ventrally near the base; and (4) the metatarsomeres are apically sinuate and lobed.

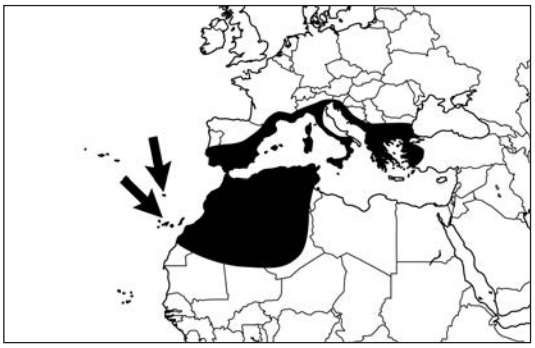
Fig. 9.16. *Meladema coriacea.* Scale = 1.0mm.

Classification. The genus is similar to *Colymbetes*, but recent analyses recover *Meladema* as sister to the Nearctic clade *Hoperius* + *Neoscutopterus* (Moriniére *et al.* 2014; Miller and Bergsten, 2014a).

Diversity. There are three species in the genus. Two of these hybridize on Tenerife based on molecular evidence (Ribera *et al.,* 2003).

Natural History. *Meladema* are characteristic of permanent streams, where they can be found in deep, clear pools. Ribera *et al.* (2003b) investigated the complicated biogeography of the genus, and the larvae have been described by Alarie and Hughes (2006). One species, *M. imbricata* (Wollaston), is very rare on the Canary Islands, restricted to only four streams (Ribera *et al.*, 2003b).

Distribution. *Meladema coriacea* Laporte is found broadly in the Mediterranean region and northwestern Africa, *M. lanio* (Fabricius) is endemic to Madeira, and *M. imbricata* is restricted to the western Canary Islands (Map 9.5).



Map 9.5. Distribution of *Meladema*.

Genus *Melanodytes* Seidlitz, 1887

Body Length. 14.0–15.0mm.

Diagnosis. *Melanodytes* differ from *Rhantus* in having the metatarsomeres I–IV apically sinuate and lobed, a narrow bead present laterally on the pronotum (Fig. 9.17), and the base of the pronotum as wide as the base of the elytra (Fig. 9.17). *Melanodytes* is very similar to *Rhantus*, but differs in having the anterior surface of the metatiba covered with setigerous punctures (Fig. 9.11a), whereas there are a few in a linear series in *Rhantus* (Fig. 9.11b).

Classification. The genus was originally described as a subgenus of *Rhantus* but has been variously treated as a subgenus (e.g., Franciscolo, 1979a) or

Fig. 9.17. *Melanodytes pustulatus.* Scale = 1.0mm.

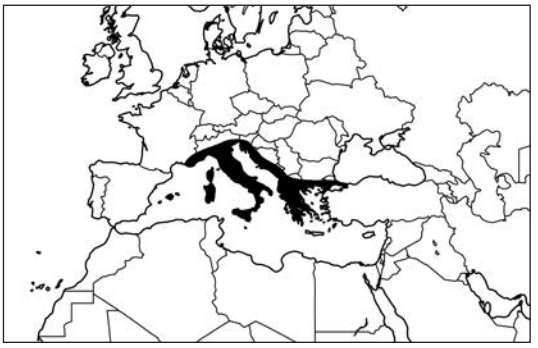
Fig. 9.18. *Neoscutopterus angustus.* Scale = 1.0mm.

a genus (e.g., de Marzo, 1974a). In recent times, it has generally been recognized as a genus (Nilsson *et al.*, 1989; Nilsson, 2001). The phylogenetic position of the genus is unclear, but some analyses suggest a relatively basal position within Colymbetinae (Ribera *et al.*, 2008; Alarie *et al.,* 2009).

Diversity. There is only a single species, *M. pustulatus* (Rossi), in the genus. It was treated by Franciscolo (1979a) and Scholtz (1927).

Natural History. Specimens are found in ponds and slow streams with vegetation (Franciscolo, 1979a). Larvae were described by de Marzo (1974a).

Distribution. *Melanodytes pustulatus* is found only in south-central Europe (Map 9.6).



Map 9.6. Distribution of *Melanodytes*.

Genus *Neoscutopterus* J. Balfour-Browne, 1943

Body Length. 13.5–16.7mm.

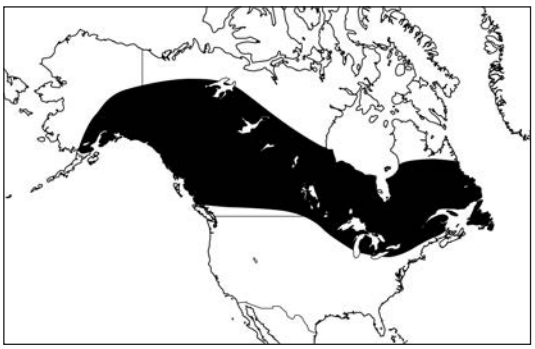
Diagnosis. This genus is characterized by the following character combination: (1) the dorsal reticulation relatively coarse and irregular (Fig. 9.8a); (2) the pronotum without a lateral bead (Figs. 9.5a,18); (3) the male protibia with a distinct emargination on the ventral margin near the base (Fig. 9.9a); and (4) the metatarsomeres with the apical marginal lobes short. Members of this group are large and robust, and piceous to black (Fig. 9.18).

Classification. *Neoscutopterus* groups into a Nearctic clade together with *Hoperius* (Ribera *et al.*, 2008; Miller and Bergsten, 2014a; Morinière *et al.*, 2014).

Diversity. There are two species in the group, *N. hornii* (Crotch) and *N. angustus* (LeConte). They can be identified using Larson *et al.* (2000).

Natural History. These species are characteristic of *Sphagnum* bogs and fens, and often in habitats with slightly flowing water. They often occur at the interface between the water and terrestrial situations such as in floating mat vegetation (Larson *et al.*, 2000). The larvae were described by Hilsenhoff (1989).

Distribution. This Nearctic taxon is transcontinental across boreal North America (Map 9.7).



Map 9.7. Distribution of *Neoscutopterus*.

Genus *Rhantus* Dejean, 1833

Body Length. 5.7–17.8mm.

Diagnosis. The genus is characterized within Colymbetinae by the following combination of characters: (1) metatarsomeres I–IV with the apical margins sinuate and lobed apically (Fig. 9.3b); (2) the prosternal process medially rounded or carinate (not flattened); (3) the marginal pronotal bead present but narrow (Figs. 9.5b,19); and (4) the anterior surface of the metatibia with only a few setigerous punctures arranged in a linear series (Fig. 9.11b). The lateral outline of most species is nearly continuous between the pronotum and elytron (Figs. 9.7b,19) except in certain rare species like *R. tristanicola* and *R. selkirki*. Specimens are often evenly brown or yellow-brown with various black markings and patterns on the pronotum and head, though some species are entirely black, and some are conspicuously marked with maculae on the elytra (Fig. 9.19).

Classification. There are currently two subgenera in the group, *Rhantus s. str.,* with nearly all of the species, and *R.* (*Nartus*), with two unicolorous black species in the Holarctic region. Several analyses have resulted in a paraphyletic *Rhantus* with respect to other genera in the tribe (Miller, 2001c; Ribera *et al.*, 2002b; 2008; Balke *et al.*, 2007a; 2009; Alarie *et al.,* 2009; Miller and Bergsten, 2014a), but without a more comprehensive analysis, it is difficult to know how to reclassify the many species. Additionally, a recent analysis by Morinière *et al.* (2014) resulted in synonymy of two genera, *Anisomeria* and *Senilites*, previously placed in their own tribe, Anisomeriini, with *Rhantus* (see above). It is likely the classification of *Rhantus* will continue to change as relationships among species and genera in the tribe are clarified.

Diversity. This is a large, complex group with 107 species currently recognized, a number likely to change as the genus is redefined. Nearctic species were revised by Zimmerman and Smith (1975b). Neotropical species were reviewed by Balke (1993b). Australian, Pacific, and Southeast Asian *Rhantus* were treated by Vazirani (1970), Watts (1978), and Balke (1993c; 1995b). Afrotropical species were addressed by Guignot (1961) and Balke (1995b). Palearctic species can be identified with Zaitzev (1953), Zimmermann and Gschwendtner (1936), Franciscolo (1979a), Balke (1990a), and Nilsson and Holmen (1995). These are not all comprehensive, however, and there have been many additional modifications to the diversity since then (Scholz, 1927; F. Balfour-Browne, 1935a; Hulden, 1982; Trémouilles, 1984; Moroni, 1988; Balke, 1989a; b; 1990b; c; 1992; 1993a; b; 1995a; 1998b; Ordish, 1989; Balke and Hendrich, 1992; Peck and Balke, 1993; Balke *et al.,* 2000a; 2002b; 2007b; 2010; Balke and Mazzoldi, 2003; Balke and Ramsdale, 2006; Zhao *et al.,* 2011; Hjalmarsson *et al.,* 2013).

Natural History. Members of *Rhantus* are found in a great many habitats from temporary pools, to ponds, to streams. Many species are particularly characteristic of ephemeral pools and other temporary habitats. Some are found at extreme elevations, such as in the high Andes where they have been collected at 5,000m (Miller, unpublished). Larvae have been described by Galewski (1963a), Nilsson (1987b), Alarie and Wang (2004), Barman *et al.* (2006), and Lemieux *et al.* (2011). Egg structure was investigated by Goodliffe (1977). Food habits have been investigated by Bosi (2001). The only example of chemical sexual signaling in a diving beetle was recently discovered in *R. suturalis* (Herbst *et al.*,

Fig. 9.19. *Rhantus* species. **a**, *R. calidus*. **b**, *R. gutticollis*. **c**, *R. atricolor*. **d**, *R. sinuatus*. Scales = 1.0mm.

2011). Smith (1973) investigated the biology and life histories of several species, and mandibular geometry was studied by Wall *et al.* (2006). The biogeographic history of the extremely widespread species *R. suturalis* was studied by Balke *et al.* (2009).

Distribution. *Rhantus* are found throughout the world (Map 9.8), including on some very remote islands such as Hawaii (Balke, 1989a), the Galápagos (Peck and Balke, 1993), and Tristan da Cuhna (Brinck, 1948).

Map 9.8. Distribution of *Rhantus*.

10. Subfamily Copelatinae

Body Length. 2.9–10.0mm.

Diagnosis. This subfamily is characterized by the following character combination: (1) the metacoxal lines are closely approximated medially (Fig. 10.1a) or absent (Fig. 10.1b); (2) the scutellum is externally visible with the elytra closed (e.g., Fig. 10.11); and (3) the metatarsal claws are subequal in length in both sexes (Fig. 10.1c). Though the metacoxal lines are absent in *Lacconectus*, *Aglymbus,* and some *Copelatus* the corresponding medial regions of the metacoxae are relatively narrow in these groups (Fig. 10.1b), suggesting that closely approximated metacoxal lines is homologous with the narrowing in these taxa. Closely approximated metacoxal lines are present also in Hydrodytinae, but this appears to be either homoplasious (Miller and Bergsten, 2014a) or intermediate between Copelatinae and Hydroporinae (Miller, 2001c).

Classification. *Copelatus* and its relatives have generally been placed within Colymbetinae, including by Sharp (1882), who placed them as one of several "unassociated" taxa in "Colymbetides." More recently the group has been recognized as its own subfamily and sister to the rest of the Dytiscidae based on *Copelatus* larvae with a foregut that includes a crop and serrated mandibles (and presumed ingestion of solid food particles) (de Marzo, 1976a; Ruhnau and Brancucci, 1984; Ruhnau, 1986; Beutel, 1994; 1998; Larson *et al.*, 2000), though larvae of most *Copelatus* and several other copelatine genera are unknown. Recent larger analyses have contradicted this proposed relationship, instead placing copelatines farther up in the phylogeny (Miller, 2001c; Ribera *et al.*, 2002b; 2008; Balke *et al.*, 2004b; 2008; Miller and Bergsten, 2014a), but there has been no consensus regarding copelatine relationships with other dytiscids. In fact, Ribera *et al.* (2008) found that Copelatinae is not monophyletic with *Agaporomorphus* related, instead, to Coptotominae. Within Copelatinae, Balke *et al.* (2004c) and Shaverdo *et al.* (2008) used mitochondrial data to test the relationships among the several genera, a couple of which, *Copelatus* and *Exocelina*, are extremely diverse at the species level (>450 and >140 species, respectively). Some results suggest that other genera, including *Lacconectus* and *Aglymbus*, are nested within *Copelatus* and that these genera are poorly defined with respect to each other as well (Balke *et al.*, 2004b; 2008). Miller and Bergsten (2014a) found Copelatinae, including *Agaporomorphus*, monophyletic with good support, and a sister-group relationships between Copelatinae and the clade Dytiscinae + (Laccophilinae + Cybistrinae), although relatively few copelatine taxa were included. Recently, Bilton *et al.* (2015) examined copelatine relationships because of discovery of a new taxon, *Capelatus*, that is evidently related to *Liopterus* and *Exocelina*. The taxonomy of Copelatinae has changed quite a bit in recent years with description of new genera, but the status of the extremely large genus *Copelatus* and several other genera remains to be adequately tested. Aside from the problematic *Copelatus*, the genera *Aglymbus* and *Lacconectus* also need clarification.

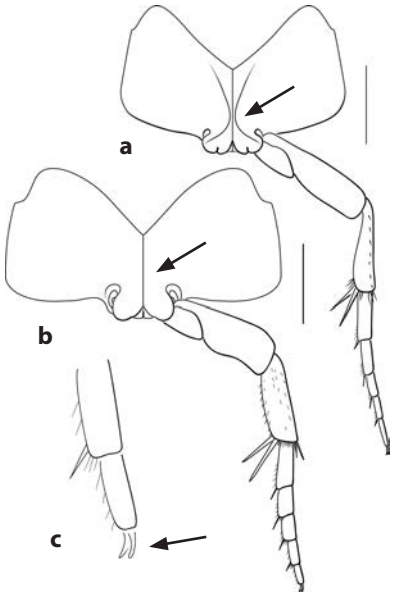


Fig. 10.1. Copelatinae features. **a**, *Copelatus caelatipennis* metacoxae and left metaleg. **b**, *Lacconectus regimbarti* metacoxae and left metaleg. **c**, *L. regimbarti* metatarsal claws. Scales = 1.0mm.

Diversity. Copelatinae currently includes eight genera, but this is likely to change as generic concepts are revised in the group.

Natural History. With a group as large and diverse as the Copelatinae, it is difficult to generalize about their natural history. These are, however, small- to medium-sized diving beetles, many of which live in relatively temporary or disturbance-prone habitats. Many occur in temporary pools, phytotelmata, forest pools, rock pools, or similar habitats that require high vagility to exploit, for which many copelatines are well adapted. Some are found only in streams. They often come to lights in large numbers and diversity, particularly during and after rains, presumably searching for new ephemeral pools. The larvae of known *Copelatus* have a crop and serrated, un-

channeled mandibles that some have interpreted as a means for ingesting solid food, which is unusual for dytisids (de Marzo, 1976a; Ruhnau and Brancucci, 1984; Ruhnau, 1986; Beutel, 1994; 1998; Larson *et al.*, 2000). Several investigators have regarded these attributes as plesiomorphies within Dytiscidae and indicative of a sister-group relationship between Copelatinae and all other Dytiscidae (see above, Beutel, 1994; 1998; Larson *et al.*, 2000). A couple of *Exocelina* (Balke *et al.*, 2004c; Watts and Humphreys, 2009), and one species of *Copelatus* (Caetano *et al.*, 2013) are subterranean, making them the only non-hydroporine subterranean dytiscids known.

Distribution. Copelatines occur throughout the world but are most diverse and abundant in tropical regions.

Key to the Genera of Copelatinae

One *Copelatus* species and two species of *Exocelina* are subterranean. These species have characteristic features of subterranean diving beetles (flightless, eyeless, depigmented) and are keyed separately in the key to subterranean taxa (page 45).

1 Metacoxal lines absent (Figs. 10.1b,2a,c) . . . 2
1' Metacoxal lines present and distinct or with at least remnants visible in most species (Figs. 10.1a,2b) 4

2(1) Metafemur without apical emargination, evenly rounded (Fig. 10.2a); apical portion of lateral lobe with lateral margins divergent, apex expanded, elongate pear-shaped (Fig. 10.3a); Southeast Asia (Map 10.6) . . *Lacconectus*, 84
2' Metafemur apically emarginate (Fig. 10.2c); lateral lobe with margins of small apical lobe subparallel (Fig. 10.3b); Afrotropical or Neotropical 3

3(2) Male with protarsomere IV with protruding anterodistal angle and with one stout, spine-like anterodistal seta (Fig. 10.4a, these features absent in *M. ruthwildae*); median lobe apically bilobed (Fig. 10.5a); Madagascar and Comoros (Map 10.8) . . . . . *Madaglymbus*, 85
3' Male with protarsomere IV not protruding and without modified seta (Fig. 10.4b); median lobe various, but not apically bilobed (Fig. 10.5b); Neotropical (Map 10.2). *Aglymbus*, 81

4(1) Dorsal surface covered with fine, short microstrioles or slightly elongated punctures (Fig. 10.6); size small, length < 3.7mm; metacoxae without strioles (Fig. 10.7a); Neotropical (Map 10.1) . . . . . *Agaporomorphus*, 80
4' Dorsal surface various, elytra with longitudinal striae, rugosity, or sometimes with fields of variable short striae; size various but usually >3.7mm, some specimens shorter; metacoxae various, but usually with strioles like fine scratches on the surface (Fig. 10.7b) 5

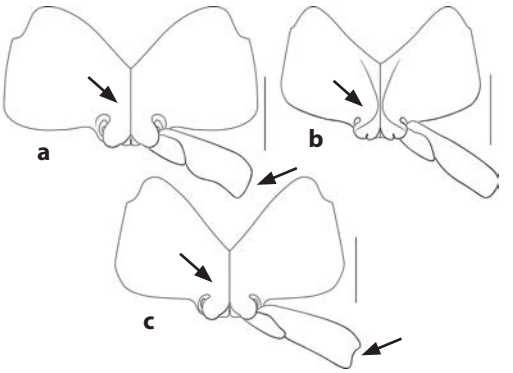


Fig. 10.2. Copelatinae metacoxae. **a**, *Lacconectus regimbarti*. **b**, *Copelatus caelatipennis*. **c**, *Aglymbus janeiroi*. Scales = 1.0mm.

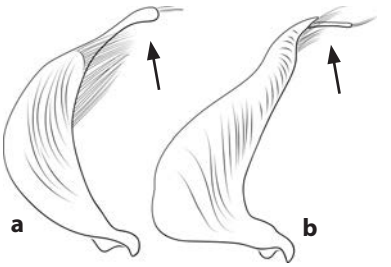


Fig. 10.3. Copelatinae right lateral lobe. **a**, *Lacconectus ritsemae*. **b**, *Aglymbus* sp.

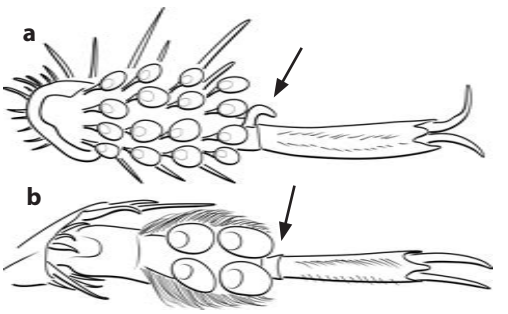


Fig. 10.4. Copelatinae left protarsi, ventral aspect. **a**, *Madaglymbus* sp. **b**, *Aglymbus janeiroi*.

Fig. 10.5. Copelatinae median lobe, ventral aspect. **a**, *Madaglymbus* sp. **b**, *Aglymbus janeiroi*. Scales = 1.0mm.

5(4) Male with anteroventral angle of protarsomere IV broadly expanded and with four large, stout spines (Fig. 10.8a); South Africa (Map 10.3) . . . . . *Capelatus*, 82

5' Male with anteroventral angle of protarsomeres IV not so broadly expanded, with single, curved spine (Fig. 10.8b) or without modifications (Fig. 10.8c) 6

6(5) With a large, distinctly hooked seta at anteroventral angle of protarsomere IV (Fig. 10.8b); Southeast Asia and Australia (Map 10.5) . . . . . *Exocelina*, 84

6' Without hooked seta, all setae at anteroventral angle of protarsomere IV small and not hooked (Fig. 10.8c) 7

7(6) Dorsal surface without longitudinal striae (Fig. 10.15); western Palearctic (Map 10.7) . . . . . *Liopterus*, 85

7' Dorsal surface with longitudinal striae (Fig. 10.12b–d), or, if without striae, then not found in western Palearctic (Map 10.4) . . . . . *Copelatus*, 82

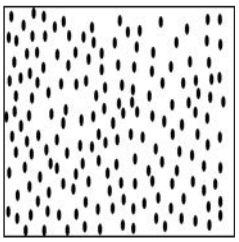


Fig. 10.6. *Agaporomorphus knischi* dorsal surface sculpture.

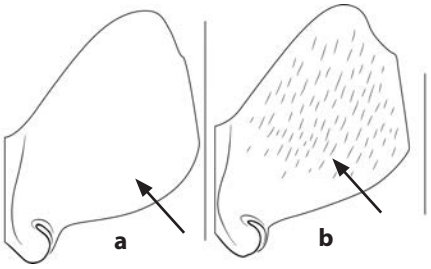


Fig. 10.7. Copelatinae left metacoxae. **a**, *Agaporomorphus knischi*. **b**, *Exocelina australiae*. Scales = 1.0mm.

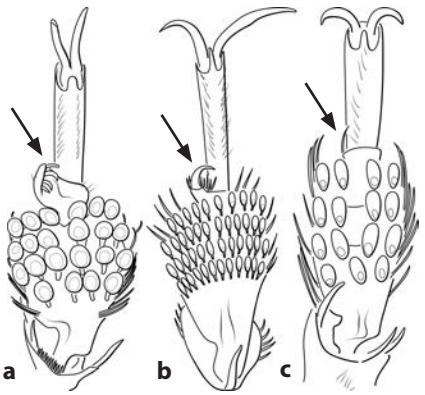


Fig. 10.8. Copelatinae left protarsi, ventral aspect. **a**, *Capelatus prykei* (drawn from Bilton *et al.*, 2015). **b**, *Exocelina melanaria*. **c**, *Copelatus distinctus*.

Genus *Agaporomorphus* Zimmermann, 1921

Body Length. 2.9–3.7mm.

Diagnosis. Within the subfamily, *Agaporomorphus* are characterized by: (1) small size (<3.7mm); (2) the metacoxae without a field of oblique, fine striae (Fig. 10.7a); (3) the dorsal surfaces of the elytra and pronotum with fine, short microstrioles (elongated punctures) evenly distributed over the surface (Fig. 10.6); and (4) the female bursa copulatrix absent. In contradiction with other earlier authors (e.g., Pederzani, 1995), members of this group do have an inconspicuous, narrow, marginal bead laterally on the pronotum. Specimens are small and dorsally brown, often with a lighter, transverse region basally on the elytron (Fig. 10.9).

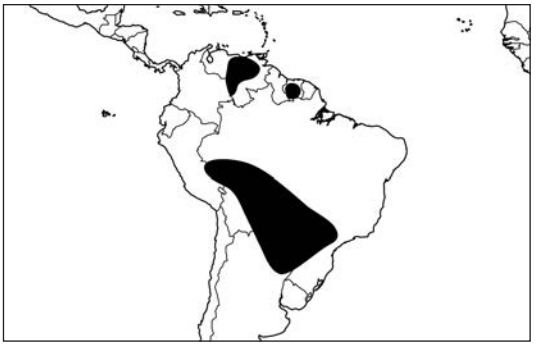
Classification. Historically, this genus also included those species now placed in *Hydrodytes* (Hydrodytinae). Evidence mainly from female genitalia (Miller, 2001c) as well as recent analyses with molecular (Ribera *et al.*, 2008) and combined data (Miller and Bergsten, 2014a) indicate the they are not related. Interestingly, Bilton *et al.* (2015) found *Agaporomorphus* sister to *Madaglymbus*.

Fig. 10.9. *Agaporomorphus knischi*. Scale = 1.0mm.

Diversity. The genus currently includes 10 known species, but new species are discovered with some regularity. They seem to be rare or, at least, rarely collected. The genus was revised by Zimmermann (1921, including *Hydrodytes* species) and Miller (2001a) with additional species described by Miller (2005b; 2014), Miller and Wheeler (2008), and Hendrich *et al.* (2015).

Natural History. Most museum specimens were collected at lights. The fewer specimens collected from aquatic habitats were found in forest pools and streams, often with heavy leaf pack. Greater details about the habitat and biology of the most recently described species, *A. julianeae* Hendrich *et al.,* was provided by Hendrich *et al.* (2015). Males of some species appear to have stridulatory devices on the abdomen. Some also have males with expanded antennomeres and others have males with modified, elongate, sinuate mesotarsal claws (Miller, 2001a), each of which may be used in male grasping of females during mating, though this has not been observed.

Distribution. This group is strictly Neotropical with species from Venezuela south to southern Brazil and southern Bolivia (Map 10.1). It is likely the group will be found to be more widespread in lowland South America as collections of these beetles increase.



Map 10.1. Distribution of *Agaporomorphus*.

Genus *Aglymbus* Sharp, 1880

Body Length. 4.2–9.0mm.

Diagnosis. Members of *Aglymbus* do not have metacoxal lines (Fig. 10.2c) like *Madaglymbus*, *Lacconectus*, and at least some *Copelatus*. From these, they differ in subtle characters such as the metafemur apically shallowly emarginate (Fig. 10.2c), the lateral lobe with the margins of the small apical lobe subparallel (Fig. 10.3b), and males with protarsomere IV not protruding and lacking modified, hooked setae (Fig. 10.4b). Many have the dorsal surface covered with short, fine strioles (Fig. 10.10). A putative character state has been the male protarsi laterally expanded with more than eight ventral adhesive setae, to differentiate especially from *Lacconectus* (e.g., Brancucci, 1986). This, however, is not reliable since some *Aglymbus* species have as few as four ventral adhesive setae (Fig. 10.4b). Specimens are elongate oval and variable in size and coloration (Fig. 10.10).

Classification. Given that reduction of the metacoxal lines has seemingly repeatedly occurred in copelatines, its likely that additional *Aglymbus* species may be found to be nested within some groups of *Copelatus* (Balke *et al.*, 2004a). The distinction between *Aglymbus* and *Lacconectus* is also not strong with the few diagnostic character states apparently

Fig. 10.10. *Aglymbus janeiroi*. Scale = 1.0mm.

unreliable (Balke *et al.*, 2004a). The genus *Rugosus* García, originally described as a colymbetinae (García, 2001), was recently synonymized with *Aglymbus* (Touissant *et al.,* 2016) after having been moved into Copelatinae (Miller and Bergsten, 2014a; Bilton *et al.,* 2015).

Diversity. With the recent removal from *Aglymbus* of several species to *Copelatus* and a new genus *Madaglymbus* (Shaverdo *et al.*, 2008), this group currently includes only 12 South American species.

Natural History. Some *Aglymbus* species are known from bromeliads (Resende and Vanin, 1991). They are also known from small forest pools.

Distribution. *Aglymbus* are Neotropical (Map 10.2).

Map 10.2. Distribution of *Aglymbus*.

Genus *Capelatus* Turner and Bilton, 2015

Body Length. 8.4–10.0mm.

Diagnosis. *Capelatus* lack long, longitudinal elytral striae but have short striae over much of the surface (Fig. 10.11). They have indistinct metacoxal lines. The main diagnostic feature is the presence of a large anteroventral expansion of the male protarsomere IV with four large ventral spines (Fig. 10.8a). This is similar to the condition in *Exocelina* (Fig. 10.8b) and *Madaglymbus* (Fig. 10.4a), but those taxa have a smaller expansion with only a single spine. *Capelatus* are large and dorsally black (Fig. 10.11).

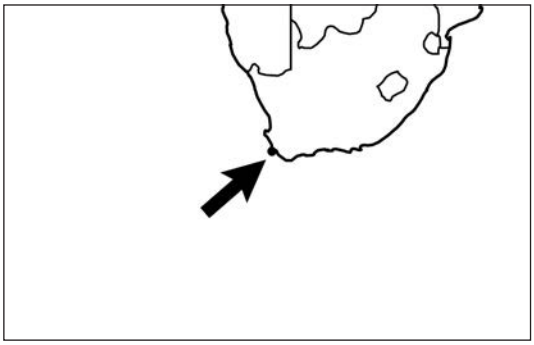
Classification. *Capelatus* was recently described for an unusual new species of Copelatinae found in an area near Cape Town, South Africa. Based on a phylogenetic analysis to place the species, it is evidently related to *Liopterus* and *Exocelina* and is a narrowly endemic relictual Cape lineage (Bilton *et al.*, 2015).

Diversity. Only one species, *C. prykei* Turner and Bilton, is included in the genus.

Fig. 10.11. *Capelatus prykei*. Scale = 1.0mm.

Natural History. Members of this group are collected only rarely from heavily vegetated semipermanent wetlands. Bilton *et al.* (2015) discussed many of the ecological correlates of the single species, as well as threats to the species because of development in the very small region in which it occurs.

Distribution. *Capelatus* are found in a very narrow area of the Cape Penninsula in Western Cape Province, South Africa (Map 10.3).



Map 10.3. Distribution of *Capelatus*.

Genus *Copelatus* Erichson, 1832

Body Length. 2.9–9.0mm.

Diagnosis. *Copelatus* have the metacoxal lines visible and distinct (Fig. 10.2b), or, more rarely, obscured or absent. There are usually a field of short strioles on the metacoxae (as in Fig. 10.7b). The dorsal surface is variable, with many species having a number of longitudinal, inscribed lines or striae (Fig. 10.12b–d, variable depending on species or species

Fig. 10.12. *Copelatus* species. **a**, *Copelatus* sp. **b**, *Copelatus* sp. **c**, *C. divisus*. **d**, *Copelatus* sp. Scales = 1.0mm.

group) or short strioles. Some species have the surface smooth, without lines or microreticulation (Fig. 10.12a). This is a large, extremely variable group that is difficult to diagnose, especially over against the complex of other copelatine genera, some of which are very similar to many *Copelatus*.

Classification. *Copelatus* is an immense, diverse group with a long history of recognition. It is not clear how other copelatine genera may be related to *Copelatus*, and it may well be that *Copelatus* as presently circumscribed is not monophyletic (Balke *et al.*, 2004a; Shaverdo *et al.*, 2008). With a better understanding of the phylogeny, several genera, including especially the large *Exocelina*, have been recently removed from *Copelatus* (Balke *et al.*, 2004a), whereas other species, such as some former *Aglymbus*, have been recently transferred into *Copelatus* (Shaverdo *et al.*, 2008). Species were organized into species groups by Guéorguiev (1968), largely based on the configuration and number of elytral striae, but it is not clear that these groups are monophyletic. It seems likely that additional changes to the genus composition of *Copelatus* will be forthcoming as the phylogeny of the group becomes better known.

Diversity. This is the largest genus in the Dytiscidae with currently 438 described species. Many more, particularly in the Neotropical region, are awaiting description, and many species groups await revision.

Natural History. *Copelatus* can be found in many water bodies, including both lentic and lotic habitats, but are particularly characteristic of ephemeral or small bodies of water from desert rock pools to shallow, leaf-choked forest pools to phytotelmata. Species are often most abundant in tropical or subtropical forests, where they may inhabit extremely small pools with only a few milliliters of water or areas where water collects in palm bracts or other, similar habitats, including bromeliads (J. Balfour-Browne, 1938; Balke *et al.*, 2008). They often come in large numbers to lights at night, especially after or during rains. One species is known from subterranean environments (a cave) (Caetano *et al.*, 2013). That species has a shortened prosternal process and other characteristics of subterranean species, but is within the definition of *Copelatus*. Larvae have been described for several species (Bertrand, 1948; Spangler, 1962a; de Marzo, 1976a; Ruhnau and Brancucci, 1984; Ruhnau, 1986; Beutel, 1994; 1998; Larson *et al.*, 2000; Mashke *et al.*, 2001).

Distribution. *Copelatus* are primarily circumtropical with the greatest diversity in Central and South America, Africa, and Southeast Asia, and on many remote islands. There are species also with ranges north to Canada and south into more temperate areas as well (Map 10.4).

Map 10.4. Distribution of *Copelatus*.

Fig. 10.13. *Exocelina australiae*. Scale = 1.0mm.

Genus *Exocelina* Broun, 1886

Body Length. 3.0–10.0mm.

Diagnosis. *Exocelina* lack longitudinal striae or shorter strioles on the elytra (Fig. 10.13), and males have a hooked seta at the anteroapical angle of protarsomere IV (Fig. 10.8b). They are dorsally typically unicolorous black to brown or reddish-brown and elongate oval (Fig. 10.13).

Classification. This group was recognized in modern times first as *Copelatus* (*Papuadytes*) Balke (1998a), and only later elevated to genus rank (Balke *et al.*, 2004a). An earlier name, *Exocelina* Broun, was discovered to have priority (Nilsson, 2007). *Exocelina* appears to be monophyletic, but its relationship with other Copelatinae is not clear (Balke *et al.*, 2004a; 2008). Bilton *et al.* (2015) found *Exocelina* sister to *Capelatus* + *Liopterus*.

Diversity. This is a large genus with currently 142 species. Many new species have been discovered and described in recent years, especially from New Guinea (Balke, 1998a; 1999; Shaverdo *et al.*, 2005; 2014) but also from elsewhere (Balke and Bergsten, 2003; Shaverdo *et al.*, 2012; Balke *et al.*, 2014).

Natural History. Most of these species are found in streams or closely associated with streams, and not in truly lentic habitats (Balke, 1998a). One species in New Guinea is found in ponds (Shaverdo *et al.*, 2013). Two species of *Exocelina* in Australia are subterranean (Balke *et al.*, 2004b; Watts and Humphreys, 2009), making these among the few nonhydroporine subterranean diving beetles known. The rich diversification in Melanesia and Australia and its biogeographic history was studied by Balke *et al.* (2007c) and Toussaint *et al.* (2014; 2015a) and inferred to be of mid-Miocene origin.

Distribution. *Exocelina* are found in Australia, New Zealand, New Guinea, and New Caledonia with disjunct species from China and Hawaii (Map 10.5).

Map 10.5. Distribution of *Exocelina*.

Genus *Lacconectus* Motschulsky, 1855

Body Length. 3.5–7.1mm.

Diagnosis. Within the subfamily, *Lacconectus* can be distinguished by: (1) the absence of metacoxal lines (Fig. 10.2a); (2) distinctive dorsal microreticulation in most species; and (3) the apical margin of the metafemur rounded (Fig. 10.2a). Brancucci (1986) was unable to find strong diagnostic character support for the group over against *Aglymbus* but provided a few additional subtle features to unite *Lacconectus*. Specimens are variable but often flattened, oval, and dorsally maculate (Fig. 10.14).

Classification. The relationship of *Lacconectus* with *Aglymbus* is not entirely clear, and putative diagnostic differences between the genera are subtle, but

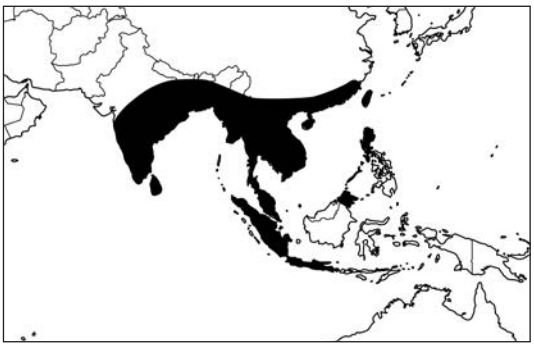
Fig. 10.14. *Lacconectus andrewesi*. Scale = 1.0mm.

they were not found to be sister groups within Copelatinae by Bilton *et al*. (2015).

Diversity. This large genus currently has 80 species. *Lacconectus* was revised by Brancucci (1986), though he and others described numerous species since then (Brancucci, 1987; 1989; 2002; 2003a–c; 2004; 2005; 2006a; b; Hendrich, 1998; Brancucci and Gusich, 2004; Brancucci and Hendrich, 2005; Hajek *et al.*, 2013).

Natural History. Most species of *Lacconectus* occur in seeps, springs, and streams, often in rocky or high-gradient areas with mineral substrates.

Distribution. This is a Southeast Asian group with representatives from India east to Taiwan and south to Java (Map 10.6).



Map 10.6. Distribution of *Lacconectus*.

Genus *Liopterus* Dejean, 1833

Body Length. 6.3–7.9mm.

Diagnosis. In *Liopterus*, the metacoxal lines are distinct (as in Fig. 10.2b), and there are no longitudinal lines on the elytra (Fig. 10.15). These are the only western Palearctic copelatines. There are many other *Copelatus* throughout the world without elytral striae (e.g., Fig. 10.12a), but not within the distribution of *Liopterus*. The group is difficult to diagnose morphologically from these *Copelatus*. Specimens are elongate oval and dorsally brown (Fig. 10.15).

Classification. Although the concept of this genus has been around for some time (see review by J. Balfour-Browne, 1939b), for much of their history the species have been treated in *Copelatus*. Within *Copelatus*, members of *Liopterus* were treated within the *C. haemorrhoidalis* group, which included all those *Copelatus* without longitudinal striae on the elytra (Guéorguiev, 1968). Balke *et al.* (2004a) resurrected *Liopterus* based on a molecular cladistic

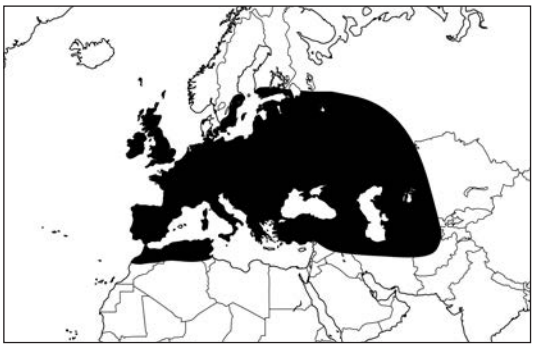
Fig. 10.15. *Liopterus haemorrhoidalis*. Scale = 1.0mm.

analysis to include only two species. As such, there are a large number of *Copelatus* without elytral striae that are difficult to diagnose from *Liopterus*.

Diversity. Two species, *L. haemorrhoidalis* (Fabricius) and *L. atriceps* (Sharp), are in the genus. They can be identified using Franciscolo (1979a).

Natural History. Members of this group have been collected from open fens with dense vegetation (Nilsson and Holmen, 1995) and lowland ponds and ditches, often in cool water (Foster and Friday, 2011). Larvae were described by de Marzo (1976a).

Distribution. *Liopterus* are found in the western Palearctic (Map 10.7).



Map 10.7. Distribution of *Liopterus*.

Genus *Madaglymbus* Shaverdo and Balke, 2008

Body Length. 4.1–9.5mm.

Diagnosis. These species lack metacoxal lines (as in

Fig. 10.16. *Madaglymbus alutaceus*. Scale = 1.0mm.

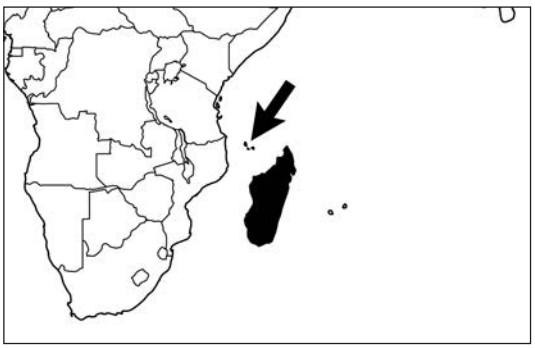
Fig. 10.1b) like *Lacconectus*, *Aglymbus,* and a few species of *Copelatus*. They can be distinguished from those genera by males with protarsomere IV protruding at the anterodistal angle and with a stout, spine-like anterodistal seta (Fig. 10.4a), though at least one species appears to lack this feature (Shaverdo *et al.*, 2008). The male median lobe is apically bilobed (Fig. 10.5a). Specimens are elongate oval, quite variable in size, and often with a dorsal color pattern (Fig. 10.16).

Classification. These species were included in *Aglymbus* until moved into a new genus by Shaverdo *et al.* (2008). *Madaglymbus* is the sister group of *Agaporomorphus* according to Bilton *et al*. (2015).

Diversity. There are currently 10 species in the genus (Shaverdo *et al.*, 2008), but recent fieldwork in Madagascar will at least double this number (Bergsten, unpublished).

Natural History. Specimens are found mainly in forest streams and adjacent pools. At least some come to lights (Shaverdo *et al.*, 2008).

Distribution. *Madaglymbus* are known from Madagascar with one species from the Comoro Islands (Map 10.8).



Map 10.8. Distribution of *Madaglymbus*.

11. Subfamily Laccophilinae

Body Length. 1.5–8.6mm.

Diagnosis. This large, distinctive, and megadiverse group is characterized by the following features: (1) both males and females have natatory setae along the posteroventral margin of the metatarsomeres but the metatibia lacks posteroventral natatory setae (Fig. 11.1, convergent or possibly homologous with Lancetinae, see Fig. 5.1a), and (2) the female gonocoxae are fused along the ventral margin with the apex pointed, and the rami are fused medially with anteriorly projecting processes and distinct ventral teeth (Fig. 11.2). The great majority of the species are in the tribe Laccophilini — many members of which are characteristically shaped, apically broad and posteriorly attenuate — and many are strikingly colorful with fasciae, maculae, and other patterns.

Classification. Laccophilinae includes Agabetini Branden, with a single genus *Agabetes* Crotch, which is sometimes recognized as its own subfamily (e.g., Burmeister, 1990), and Laccophilini Gistel, which includes the bulk of the diversity in the subfamily. Placement of *Agabetes* (or Agabetini) with the other laccophilines has been confirmed in more recent analyses (Miller, 2001c; Alarie *et al.*, 2002b; Miller and Bergsten, 2014a). There has been no general consensus of relationships of Laccophilinae with other dytiscid groups, though they were historically often placed with "Noterinae" before that group was removed from Dytiscidae (e.g., Sharp, 1882). Larval evidence (Ruhnau and Brancucci, 1984) and female reproductive musculature (de Marzo, 1997) have suggested some affinities with Hydroporinae, and Nilsson (1989b) raised the possibility of close relationship with Lancetinae. A monophyletic Laccophilinae was found to be sister to Cybistrinae with good support in a recent analysis by Miller and Bergsten (2014a), rendering Dytiscinae, as historically understood, paraphyletic. Despite this seemingly odd relationship, a close affinity between Laccophilinae, Cybistrinae, and Dytiscinae is perhaps not unreasonable given that these taxa have (at least plesiomorphically) endophytic oviposition

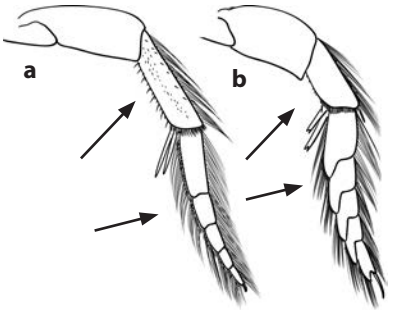


Fig. 11.1. Laccophilinae metalegs. **a**, *Agabetes acuductus*. **b**, *Laccophilus hyalinus*.

with fused and knife-like ovipositors (Fig. 11.2).

Diversity. Two tribes and fourteen genera are included.

Natural History. The majority of laccophiline genera are found in the margins of small streams, except *Africophilus* which are in hygropetric habitats, and *Laccophilus,* which are found in most habitats diving beetles occur, lotic and lentic. No laccophilines have yet been found in subterranean waters.

Distribution. This group is extremely widespread throughout the world. There are distinct faunas in every biogeographic region with numerous endemic genera as well as other groups, particularly *Laccophilus*, that are extremely widespread and successful across many regions.

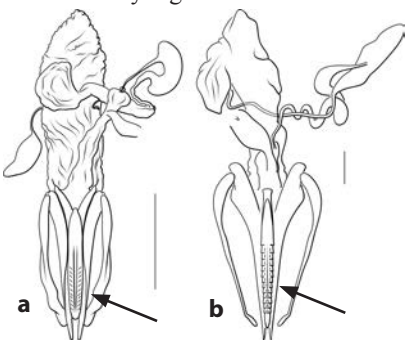


Fig. 11.2. Laccophilinae female genitalia, ventral aspect. **a**, *Agabetes acuductus*. **b**, *Laccomimus* sp. Scales = 1.0mm (a) and 0.1mm (b).

Key to the Tribes of Laccophilinae

1 With two metatarsal claws (Fig. 11.3a); scutellum visible with elytra closed (Fig. 11.4a); metatarsomeres I–IV without distinct posterolateral lobes (Fig. 11.5a) . . . . . Agabetini, 89

Fig. 11.3. Laccophilinae metatibial claws. **a**, *Agabetes acuductus*. **b**, *Laccophilus hyalinus*.

1' Scutellum concealed and not visible with elytra closed (Fig. 11.4b); with one metatarsal claw (Fig. 11.3b); metatarsomeres I–IV with large, distinct posterolateral lobes (Fig. 11.5b,c) . . . . . Laccophilini, 91

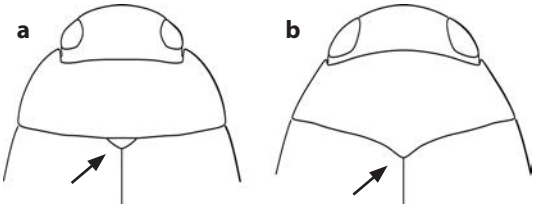


Fig. 11.4. Laccophilinae heads and pronota. **a**, *Agabetes acuductus*. **b**, *Laccophilus fasciatus*.

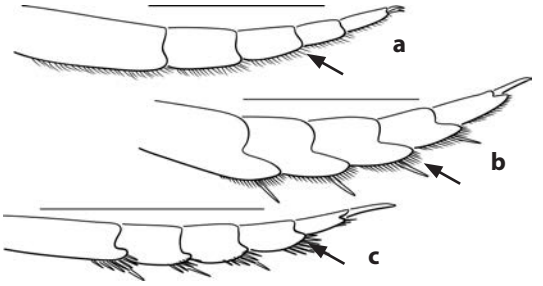


Fig. 11.5. Laccophilinae metatibiae. **a**, *Agabetes acuductus*. **b**, *Laccophilus proximus*. **c**, *Neptosternus* sp. Scales = 1.0mm.

12. Tribe Agabetini

Body Length. 6.0–7.5mm.

Diagnosis. From Laccophilini, agabetines are distinct in having: (1) a visible scutellum with the elytra closed (Fig. 12.3); (2) two subequal metatarsal claws (see Fig. 11.3a); and (3) weakly lobed metatarsomeres (see Fig. 11.5a). These are medium-sized, darkly colored, oval beetles that are superficially similar to certain agabines and copelatines (Fig. 12.3), but lack a series of closely placed setae at the apical angle of the metafemur and have the distinct metacoxal lines broadly separated, among other things. In addition, the dorsal surface is covered with short, fine, longitudinal strioles (Fig. 12.1), and males have a distinctive pair of longitudinal, parallel grooves on abdominal sternum VI (Fig. 12.2a, males of *A. svetlanae* Nilsson are not known).

Classification. *Agabetes* has a long history of ambiguity in its classification. Originally placed as a tribe in Colymbetinae, the single historically known species has also been placed in Copelatinae (Zimmermann, 1920; Guéorguiev, 1968). Burmeister (1976; 1990) discovered character states in the female genitalia that strongly support a close relationship between *Agabetes* and Laccophilinae, including fused gonocoxae and serrated, fused rami (Fig. 12.2b), though he believed the two groups to be distinct enough for each to have subfamilial rank. This relationship was further corroborated by Ruhnau and Brancucci (1984) and Nilsson (1989b), and later supported by evidence from larval features (Alarie *et al.*, 2002b); though some molecular analyses have contradicted the relationship (e.g., Ribera *et al.*, 2008), others support it (Miller and Bergsten, 2014a). Although some subsequent authors have also recognized *Agabetes* in a group at family rank (e.g., Larson *et al.*, 2000), others (e.g., Miller, 2001c), in recognition of the relationship between the groups, have instead accepted two tribes, Agabetini and Laccophilini, in one subfamily, Laccophilinae (Miller and Bergsten, 2014a).

Diversity. *Agabetes* is the only genus in the tribe.

Natural History. See below under *Agabetes*.

Distribution. See below under *Agabetes*.

Fig. 12.1. *Agabetes acuductus* elytral sculpture.

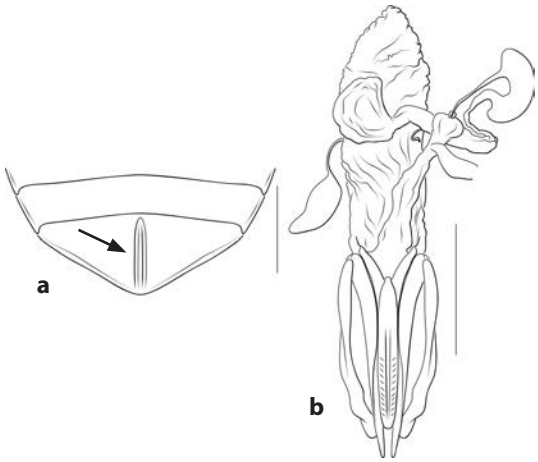


Fig. 12.2. Agabetini features. **a**, *Agabetes acuductus* male abdominal apex, ventral aspect. **b**, *A. acuductus* female genitalia. Scales = 1.0mm.

Genus *Agabetes* Crotch, 1873

Diagnosis. This is the only genus in the tribe, and it is characterized by its diagnostic features. Specimens are medium sized, oval, and dark brown to brownish-red (Fig. 12.3).

Classification. *Agabetes acuductus* (Harris) was described in the genus *Colymbetes*, but Crotch (1873) placed it in his new genus *Agabetes*. The genus was placed in different groups including Colymbetinae and Copelatini until Burmeister (1990) convincingly placed it as sister to Laccophilinae based in large part on the female genitalia.

Diversity. Two species are known in this genus, *A. acuductus* and *A. svetlanae*. The genus included only a single species for most of its taxonomic history, but a new one from Iran was described in modern times, based on five female specimens collected in 1915, and it is very similar to the North American species (Nilsson, 1989b).

Natural History. *Agabetes acuductus* specimens are typically found in shaded pools in deciduous forests (Young, 1954). Some populations or specimens may

Fig. 12.3. *Agabetes acuductus*. Scale = 1.0mm.

be flightless, though there are records of specimens at lights, suggesting at least some individuals can fly (Young, 1954). The larvae of *A. acuductus* were described by Spangler and Gordon (1973) and Alarie *et al.* (2002b). Nothing is known of the biology of *A. svetlanae*.

Distribution. The two species in the group have dramatically disjunct distributions with one species, *A. acuductus,* fairly widespread in eastern North America, and the other species, *A. svetlanae*, from the Caspian coast of Iran (Map 12.1).

Map. 12.1. Distribution of *Agabetes*.

13. Tribe Laccophilini

Body Length. 1.5–8.6mm.

Diagnosis. This tribe is easily diagnosed from Agabetini by (1) the scutellum not visible with the elytra closed (see Fig. 11.4b), (2) a single metatarsal claw (see Fig. 11.3b), and (3) prominent lobes at the apices of metatarsomeres I–IV (see Figs. 11.5b,c,13.1). These lobes are distinctive, though they are relatively shorter in *Neptosternus* and *Philaccolus*. Laccophilines are minute to medium-sized, compact beetles. They are often broad anteriorly and tapered posteriorly to a point (e.g., Fig. 13.16). Many species are marked with distinct longitudinal lines, maculae, fasicae, or other more complex markings, though others are more simple or concolorous.

Classification. There has been little historical controversy about the naturalness of this group as defined here. What has been more controversial is its association with other Hydradephaga. Its relationship with Agabetini is a relatively new conclusion dating to Burmeister (1990). Historically, the group was placed together with Noteridae in the *Dytisci fragmentati* (Sharp, 1882) based on laterally closed mesocoxal cavities (the metepisternum not extending to the mesocoxal cavity). Noterids were later moved out of Dytiscidae, and laccophilines were then thought to be possibly related to Lancetinae (Nilsson, 1989b). Relationships among genera are largely unknown. The group is in great need of careful phylogenetic revision at the genus level.

Diversity. The tribe is a diverse, large, and species-rich group with 13 currently recognized genera. A new genus has recently been described (Toledo and Michat, 2015). It includes both megadiverse genera like *Laccophilus* (>280 species) and genera with only one to a handful of species.

Natural History. Members of this group occur in a broad range of habitats from typical ponds and marshes to rivers and streams. They are known from temporary habitats and phytotelmata, such as where water collects in palm bracts on the forest floor, muddy pools in roads, and desert rock pools. Some, such as *Africophilus*, are hygropetric. Many genera, like *Australphilus* and *Philaccolilus*, are restricted to streams. Most members of the group are able to jump using the hind legs. They lock a notch on the dorsal side of the metafemur into a small, triangular projection on the medial portion of the metacoxa (Fig. 13.1), then release the tension stored in the legs to spring upward and forward.

Distribution. This is a primarily tropical group, though there are temperate-latitude or high-elevation representatives, especially in *Laccophilus*. Many of the genera are endemic to major biogeographic regions, though *Laccophilus*, a notable exception, is found worldwide. Some *Laccophilus* are found in very remote habitats and localities.

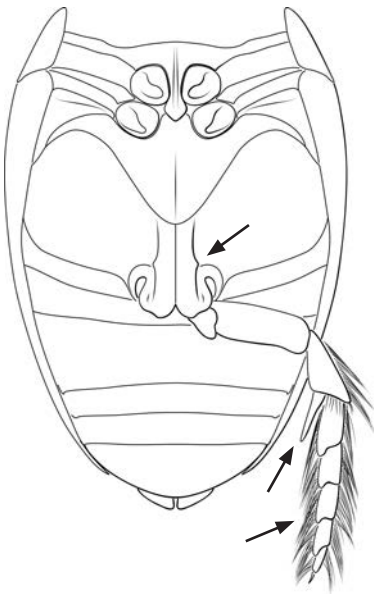


Fig. 13.1. *Napodytes boki* ventral surface. Scale = 1.0mm.

Key to the Genera of Laccophilini

1 Metatibia with single, large apical spur (Fig. 13.1); male with medial antennomeres laterally expanded (Fig. 13.2a), dimorphic, female antennomeres not expanded; Neotropical (Map 13.9) . . . . . *Napodytes*, 99

1' Metatibia with two apical spurs (Fig. 13.4a); male and female antennomeres similar, neither medially expanded (Fig. 13.2b) 2

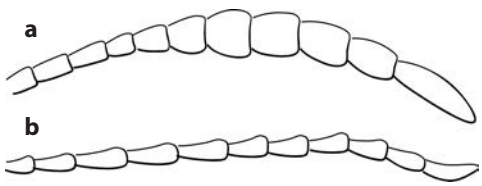


Fig. 13.2. Laccophilini right antenna. **a**, *Napodytes boki*. **b**, *Neptosternus* sp.

2(1) Metatibial spurs (at least anterior spur) apically bifid (Fig. 13.4a); worldwide (Map 13.6) . . . . . *Laccophilus*, 96
2' Metatibial spurs simple (Fig. 13.4b) 3

3(2) Prosternal process apically trifid (Fig. 13.3a); Afrotropical and Southeast Asia (Map 13.10) . . . . . *Neptosternus*, 99
3' Prosternal process apically simple (Fig. 13.3b–d) 4

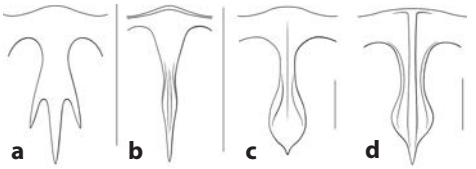


Fig. 13.3. Laccophilini prosternal processes. **a**, *Neptosternus* sp. **b**, *Philodytes umbrinus*. **c**, *Japanolaccophilus niponensis*. **d**, *Laccodytes neblinae*. Scales = 1.0mm (a,b) and 0.1mm (c,d).

4(3) Posteromedial margin of pronotum posteriorly angulate (Fig. 13.5a) 5
4' Posteromedial margin of pronotum straight or nearly straight (Fig. 13.5b) 10

5(4) Prosternal process laterally compressed, elongate, and apically pointed (Fig. 13.3b) 6
5' Prosternal process not laterally compressed, broader, but apex sometimes pointed (Fig. 13.3c,d) 7

6(5) Surfaces of legs conspicuously and densely punctate, setose (Fig. 13.6a); length < 5mm; Tibet (Map 13.7) . . . . . *Laccoporus*, 97
6' Surfaces of legs not punctate (Fig. 13.6b); length > 5mm; Afrotropical (Map 13.13) . . . . . *Philodytes*, 101

7(5) Metacoxal lines approximately straight, nearly parallel (Fig. 13.7a,b) 8
7' Metacoxal lines sinuate and/or convergent anteriorly (Fig. 13.7c,d). 9

8(7) Body short and broad, abruptly narrowed posteriorly (Fig. 13.17); prosternal process broad and triangular behind procoxae with apex short and broadly acuminate (Fig. 13.3c); female with last abdominal ventrite not lobed or emarginate (Fig. 13.8a); east Palearctic (Map 13.3). . . . . .*Japanolaccophilus*, 95
8' Body elongate, less narrowed posteriorly (Fig. 13.18); prosternal process various, but generally with apex elongate acuminate (Fig. 13.3d); female with last abdominal ventrite bilobed or medially emarginate (Fig. 13.8b); Neotropical (Map 13.4) . . . . . *Laccodytes*, 95

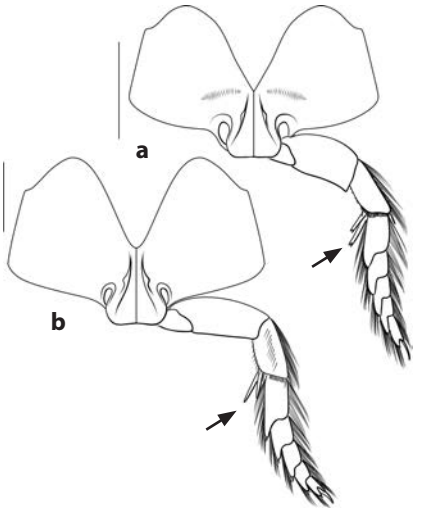


Fig. 13.4. Laccophilini metacoxae and left metaleg. **a**, *Laccophilus hyalinus*. **b**, *Philodytes umbrinus*. Scales = 1.0mm.

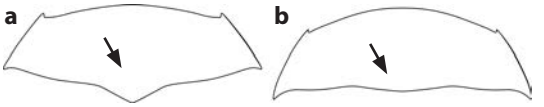


Fig. 13.5. Laccophilini pronotum. **a**, *Philodytes umbrinus*. **b**, *Philaccolus* sp.

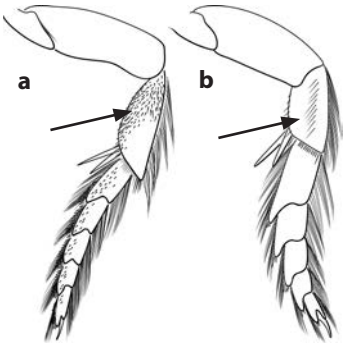


Fig. 13.6. Laccophilini left metaleg. **a**, *Laccoporus nigritulus*. **b**, *Philodytes umbrinus*.

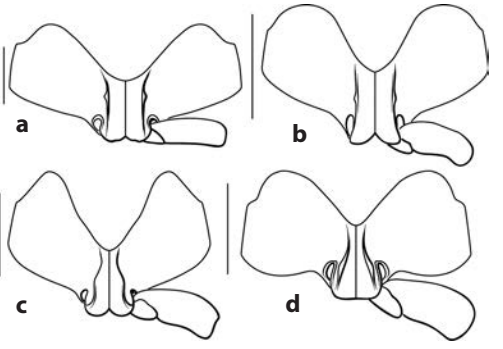


Fig. 13.7. Laccophilini metacoxae and left metatrochanter and metafemur. **a**, *Japanolaccophilus niponensis*. **b**, *Laccodytes apalodes*. **c**, *Laccomimus* sp. **d**, *Africophilus nesiotes*. Scales = 0.5mm.

9(7) Mesotibial spurs shorter than or equal to length of mesotarsomeres I–II (Fig. 13.9a); elytra covered with numerous, fine impressed punctures; Southeast Asia (Map 13.8) . . . . . *Laccosternus*, 98

9' Mesotibial spurs longer than mesotarsomeres I–IV (Fig. 13.9b); elytra impunctate or nearly so; Neotropical and southeast Nearctic (Map 13.5). . . . . *Laccomimus*, 96

10(4) Elytra microreticulation composed of large elongate or polygonal cells (Fig. 13.10a); male abdominal sternites V–VI asymmetically modified, V with medial, marginal triangular protrusion, VI with medial depression, apically variably emarginate with pencils of hairs (Fig. 13.11); metacoxal lines strongly convergent anteriorly (Fig. 13.7d); Afrotropical, including Madagascar (Map 13.1). . . . *Africophilus*, 94

10' Elytra microreticulation composed of small transverse cells (Fig. 13.10b); male abdominal sternites not modified; metacoxal lines slightly to distinctly convergent anteriorly (Fig. 13.7c) 11

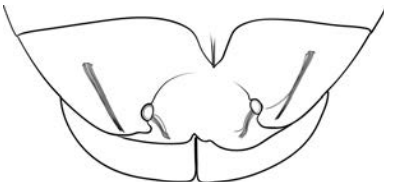


Fig. 13.11. *Africophilus nesiotes*, male terminal abdominal sternites.

11(10) Space between metacoxal lines strongly rugose-punctate; metacoxal process posteriorly multilobed (Fig. 13.12a); southeastern Australia (Map 13.2) . . . . . *Australphilus,* 94

11' Space between metacoxal lines approximately smooth; metacoxal process posteriorly bilobed or nearly straight (Fig. 13.12b,c). 12

12(11) Metacoxa with stridulatory file (Fig. 13.12b); posterolatral lobes of metatarsi short (Fig. 13.13a); female ventrite VI apically rounded (Fig. 13.14a); Afrotropical, including Madagascar (Map 13.12). . . *Philaccolus*, 100

12' Metacoxa without stridulatory file (Fig. 13.12c); posterolateral lobes of metatarsi very long (Fig. 13.13b); female ventrite VI apically lobed (Fig. 13.14b); New Guinea (Map 13.11) . . . . . *Philaccolilus*, 100

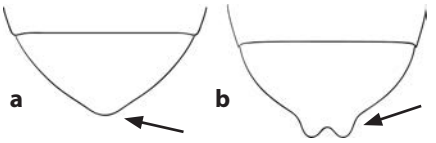


Fig. 13.8. Laccophilini female last abdominal ventrites. **a**, *Japanolaccophilus niponensis*. **b**, *Laccodytes apalodes*.

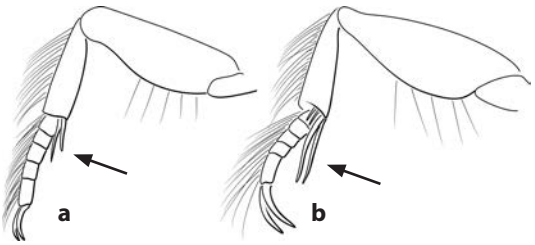


Fig. 13.9. Laccophilini mesolegs. **a**, *Laccosternus krausi*. **b**, *Laccomimus* sp.

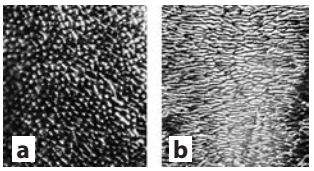


Fig. 13.10. Laccophilini elytral surface sculpture. **a**, *Africophilus* sp. **b**, *Philaccolus* sp.

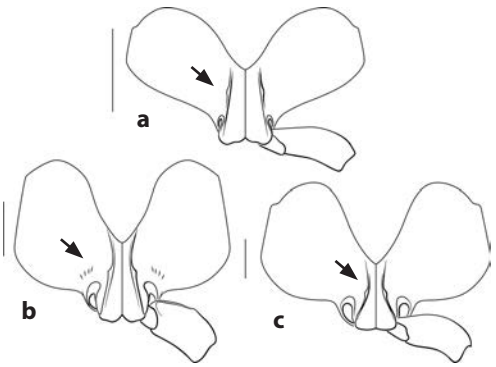


Fig. 13.12. Laccophilini metacoxae and left metafemur. **a**, *Australphilus saltus*. **b**, *Philaccolus* sp. **c**, *Philaccolilus bellissimus*. Scales = 0.5mm.

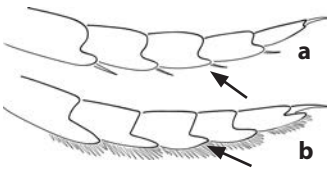


Fig. 13.13. Laccophilini metatarsi. **a**, *Philaccolus* sp. **b**, *Philaccolilus bellissimus*.

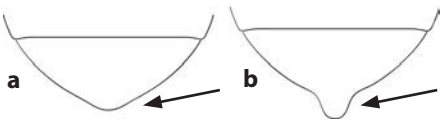


Fig. 13.14. Laccophilini female abdominal ventrite VI. **a**, *Philaccolus* sp. **b**, *Philaccolilus bellissimus*.

Fig. 13.15. *Africophilus differens*. Scale = 1.0mm.

Genus *Africophilus* Guignot, 1948

Body Length. 1.6–3.4mm.

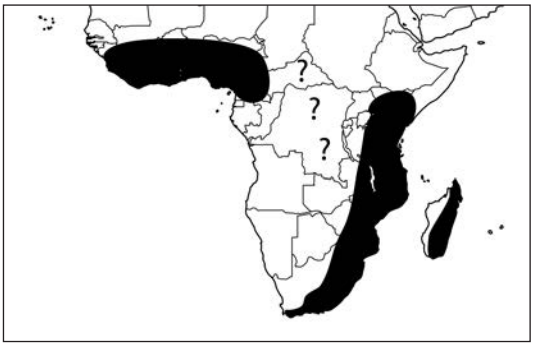
Diagnosis. *Africophilus* are small, rounded, typically dark-colored diving beetles, though many have small pale subapical markings on the elytra (Fig. 13.15). The elytral reticulation is usually conspicuous and composed of large cells (Fig. 13.10a). The metacoxal lines are strongly convergent anteriorly (Fig. 13.7d), and the posterior margin of the pronotum is straight (Fig. 13.15). Males have abdominal sternites V and VI asymmetrically modified with clusters of setae and irregular sculpturing (Fig. 13.11).

Classification. *Africophilus* is an internally homogeneous genus, but relationships with other laccophilines are uncertain.

Diversity. There are currently 18 described species in this taxon, but most are relatively poorly known. Given their habitat, poorly collected rock-face seeps (see below), it seems likely that new species will be discovered as this habitat becomes better collected in Africa. Numerous new species are known from Madagascar, for example (Bergsten, unpublished).

Natural History. Many *Africophilus* are found in hygropetric habitats and are the only laccophilines known from these habitats. They can also be found in gravel along margins of mountain streams (Omer-Cooper, 1969). Although all Laccophilini jump, these are particularly adept at jumping on the rocks where they occur, making them difficult to collect.

Distribution. The species in this group are Afrotropical (Map 13.1).



Map 13.1. Distribution of *Africophilus*.

Genus *Australphilus* Watts, 1978

Body Length. 2.4–2.7mm.

Diagnosis. *Australphilus* are small and similar to other small laccophilines except: (1) the elytral microreticulation is composed of small, transverse cells (as in Fig. 13.10b); (2) the metacoxal lines are slightly convergent anteriorly (Fig. 13.12a); and (3) the posterior margin of the pronotum is straight (Fig. 13.16). *Australphilus* are small, attractively marked beetles (Fig. 13.16).

Classification. Watts (1978) speculated that *Australphilus* might be closest to *Philaccolus,* but it is grouped with *Laccodytes* in Ribera *et al*. (2008).

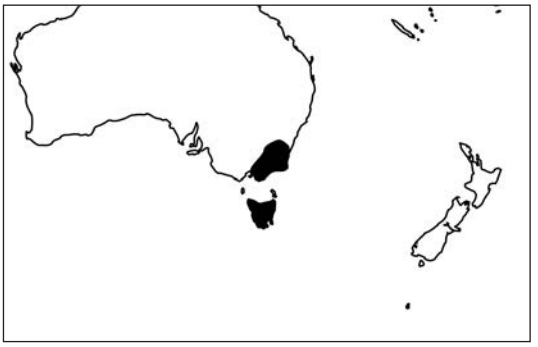
Diversity. Two species are assigned to this genus, *A. saltus* Watts and *A. montanus* Watts. They can be identified using the key by Watts (1978).

Natural History. *Australphilus* are found along the

Fig. 13.16. *Australphilus saltus*. Scale = 1.0mm.

edges of small mountain streams.

Distribution. These dytiscids are found in extreme southeastern Australia, especially in the Great Dividing Range, and Tasmania (Map 13.2).



Map 13.2. Distribution of *Australphilus*.

Genus *Japanolaccophilus* Satô, 1972

Body Length. 3.0–3.2mm.

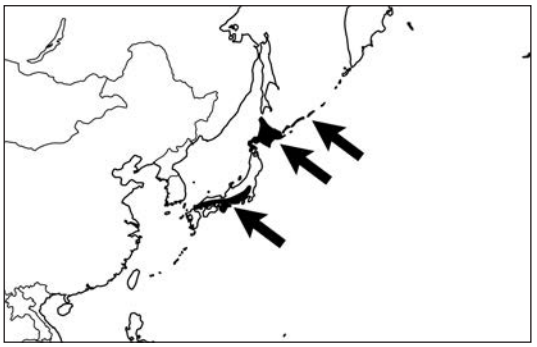
Diagnosis. *Japanolaccophilus* are characterized by the following: (1) presence of two metatibial spurs that are apically simple (as in Fig. 13.4b); (2) the prosternal process is moderately broad, not laterally compressed, and apically acute (Fig. 13.3c); (3) the posteromedial margin of the pronotum is angulate (Fig. 13.17); and (4) the metacoxal lines are subparallel (Fig. 13.7a). These beetles are moderately large for the group (length > 2.5mm) and are dorsally distinctly maculate (Fig. 13.17).

Classification. The included species was originally described in *Neptosternus*, but relationships of the genus are uninvestigated.

Diversity. There is a single species in the genus, *J. niponensis* (Kamiya).

Natural History. *Japanolaccophilus* are rare (and considered endangered) and generally found in running water (Satô, 1972; Okada, 2009).

Distribution. These beetles are found only in Japan (Map 13.3).



Map 13.3. Distribution of *Japanolaccophilus*.

Genus *Laccodytes* Régimbart, 1895

Body Length. 1.5–2.4mm.

Diagnosis. Within Laccophilini, *Laccodytes* are characterized by: (1) the metatibial spurs apically simple (as in Fig. 13.4b); (2) the prosternal process moderately broad and apically simple and acuminately pointed, not laterally compressed (Fig. 13.3d); (3) the posteromedial margin of the pronotum angulate (Fig. 13.18); (4) the posterolateral angles of the pronotum obtusely angulate to sharply pointed (Fig.

Fig. 13.17. *Japanolaccophilus niponensis*. Scale = 1.0mm.

Fig. 13.18. *Laccodytes apalodes*. Scale = 1.0mm.

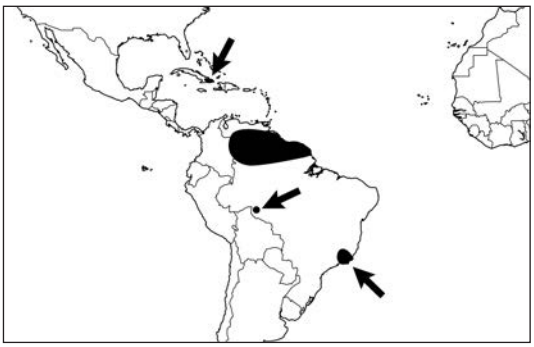
13.18); and (5) the metacoxal lines somewhat divergent anteriorly (Fig. 13.7b). Specimens are very small (length < 2.5mm), and often dorsally maculate and fasciate (Fig. 13.18). Females have the apical abdominal ventrite bilobed or with a U- or V-shaped medial emargination (Fig. 13.8b).

Classification. Steiner (1981) thought *Napodytes* and *Laccodytes* may be related. Toledo *et al.* (2010) thought that both might be related to *Neptosternus*, though *Laccodytes* and *Australphilus* are grouped together in the analysis by Ribera *et al.* (2008).

Diversity. *Laccodytes* currently includes 11 species after a species historically placed in *Laccodytes* was removed and placed with numerous new ones in *Laccomimus* (Toledo and Michat, 2015). The genus was revised by Toledo *et al.* (2010) and a subsequent new species was described by Toledo *et al.* (2011).

Natural History. *Laccodytes* occur primarily in lowland tropical and subtropical streams, often in marginal leaf packs (Toledo *et al.*, 2010).

Distribution. *Laccodytes* are found in northern South America (the Guiana Shield), across Brazil and also in Cuba (Map 13.4).



Map 13.4. Distribution of *Laccodytes*.

Genus *Laccomimus* Toledo and Michat, 2015

Body Length. 1.8–2.5mm.

Diagnosis. This genus is characterized by the combination of the following: (1) the two metatibial spurs apically simple (as in Fig. 13.4b), (2) the base of the pronotum medially angulate (Fig. 13.19), (3) the prosternal process relatively short and apically rounded, (4) the dorsal surface nearly impunctate (Fig. 13.19), and (5) the mesotibial spurs longer than mesotarsomeres I–IV (Fig. 13.9b). Specimens are robust and posteriorly narrowed with most species dorsally indistinctly maculate (Fig. 13.19).

Fig. 13.19. *Laccomimus* sp. Scale = 1.0mm.

Classification. *Laccomimus* is sister to *Laccosternus* (Toledo and Michat, 2015).

Diversity. This is a recently erected genus for 12 species, 11 new and 1 previously placed in *Laccodytes* (Toledo and Michat, 2015). The species are similar to each other, but the revision by Toledo and Michat (2015) allows for their identification.

Natural History. Little has been published about the natural history of *Laccomimus* species. Toledo and Michat (2015) report that many specimens were collected at light and others were collected from lentic habitats. Young (1954) described the habitat for the Florida species as shaded areas of a permanent pond.

Distribution. Species are found from Florida and central Mexico south through Central America, the Carribean and lowland South America (Map 13.5).

Map 13.5. Distribution of *Laccomimus*.

Genus *Laccophilus* Leach, 1815

Body Length. 1.8–8.6mm.

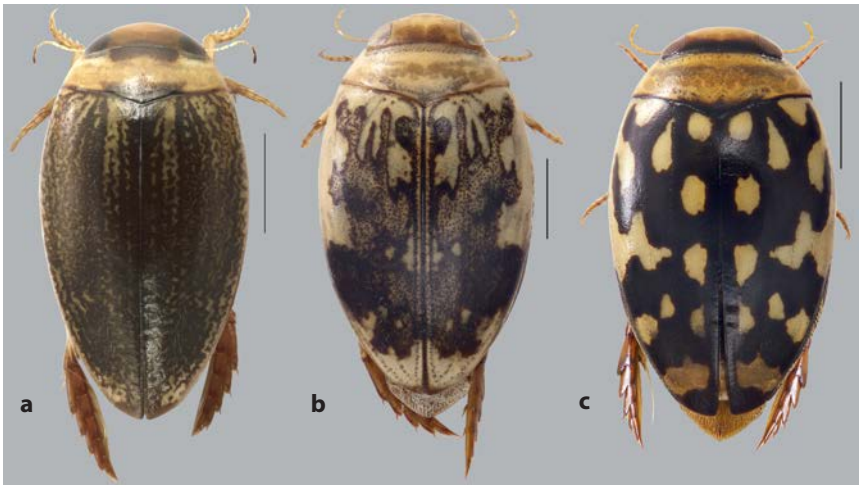


Fig. 13.20. *Laccophilus* species. **a**, *L. congener.* **b**, *L. fasciatus*. **c**, *L. pictus*. Scales = 1.0mm.

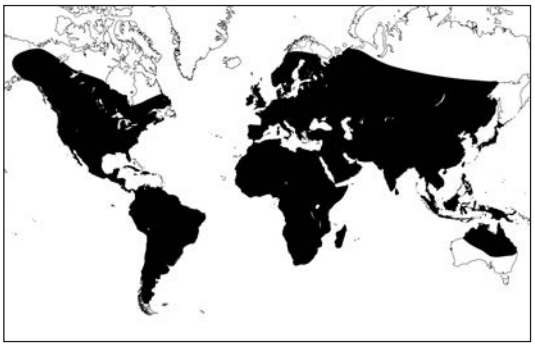
Diagnosis. This genus, although the largest and most diverse in the subfamily, and one of the largest in all diving beetles, is easily diagnosed within the tribe by the presence of two apically bifid metatibial spurs (Fig. 13.4a). However, one exception — *L. bapak* Balke, Larson, and Hendrich evidently nested in *Laccophilus,* but with simple metatibial spurs — is known and discussed by Balke *et al.* (1997b). Other features are more variable, but include the presence in many species of a stridulatory device in the form of a series of closely spaced ridges (file) on the metacoxa that interfaces with a ridge on the posterior surface of the metafemur (Fig. 13.4a). This is usually only in male specimens, but in some species it occurs on both males and females. Species are quite variable in coloration (Fig. 13.20).

Classification. It is possible that several of the genera in Laccophilinae with simple metatibial spurs, which are otherwise very similar to *Laccophilus*, are nested within this genus. These include *Philodytes* and *Laccoporus*, each of which eventually may be found to be *Laccophilus* species with simple metatibial spurs (Balke *et al.*, 1997b; Zhao *et al.*, 2011).

Diversity. With currently 282 species, this is the second most species-rich genus in all the Dytiscidae. The group has not been comprehensively revised, but faunas of several regions have been treated entirely, including the Nearctic (Zimmerman, 1970), the Afrotropical (Omer-Cooper, 1958a; Guignot, 1959b; Biström *et al*., 2015), the Palearctic, Oriental, and Australian regions (Watts, 1978; Brancucci, 1983b; Balke *et al.*, 1997b) and India (Vazirani, 1968). The Neotropical fauna, with at least 100 known species, has, significantly, never been revised.

Natural History. Species in this group occur in many habitats, from typical lotic and lentic situations to phytotelmata, springs, seeps, and many other circumstances. Larvae of several species have been described (de Marzo, 1976b; Galewski, 1978a; Hagenlund and Nilsson, 1985; Sizer *et al.*, 1998; Shaverdo, 1999). Prothoracic defensive gland products have been investigated (Schildknecht *et al.*, 1983; Baumgarten *et al.*, 1997; Schaaf *et al.*, 2000), and life history studies and other aspects of the biology and ecology of some species have been studied (Hodgson, 1951; Zimmerman, 1959; 1960; Roberts *et al.*, 1967; Hagenlund and Nilsson, 1985; Pal and Ghosh, 1993; Sizer *et al.*, 1998; Padma Sridharan and Issaque Madani, 2000).

Distribution. This group has major faunas in every biogeographic region (Map 13.6).



Map 13.6. Distribution of *Laccophilus*.

Genus *Laccoporus* J. Balfour-Browne, 1939

Body Length. 4.5–5.0mm.

Diagnosis. *Laccoporus* have: (1) the metatibial spurs

Fig. 13.21. *Laccoporus nigritulus*. Scale = 1.0mm.

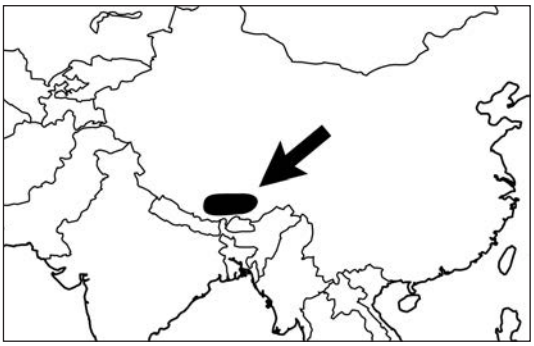
apically simple (as in Fig. 13.4b); (2) the posteromedial margin of the pronotum angulate (Fig. 13.21); (3) the prosternal process elongate, slender, and apically simple and pointed (as in Fig. 13.3b); and (4) the surfaces of the legs densely punctate (Fig. 13.6a). Specimens of the single species are very similar to *Laccophilus* but have simple metatibial spurs. They are dorsally uniformly yellow-brown and ventrally black with yellow-brown legs, epipleura, and portions of the abdominal sterna (Fig. 13.21).

Classification. Little is known of relationships of *Laccoporus* with other laccophilines. The genus may prove to be a *Laccophilus* with simple metatibial spurs (Zhao *et al.*, 2011).

Diversity. Only one species is currently recognized in this obscure genus, *L. nigritulus* (Gschwendtner). The name *L. viator* J. Balfour-Browne was recently synonymized with *L. nigritulus* (Zhao *et al*., 2011).

Natural History. Nothing is known of the natural history of *L. nigritulus*.

Distribution. *Laccoporus* are found only in Tibet near the Tibet/Nepal border (Map 13.7).



Map 13.7. Distribution of *Laccoporus*.

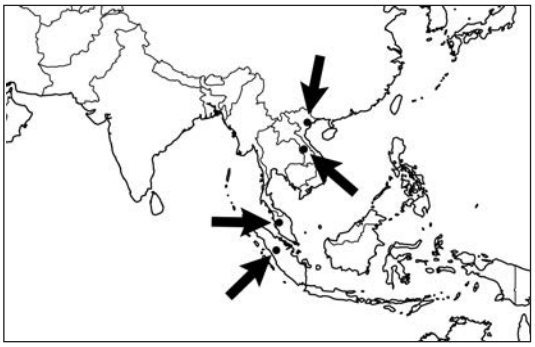
Fig. 13.22. *Laccosternus krausi*. Scale = 1.0mm.

Genus *Laccosternus* Brancucci, 1983

Body Length. 2.4–2.6mm.

Diagnosis. This genus is characterized by the combination of the following: (1) the two metatibial spurs apically simple (as in Fig. 13.4b), (2) the base of the pronotum medially angulate (Fig. 13.22), (3) the prosternal process relatively short and apically rounded, (4) the dorsal surface punctate (Fig. 13.22), and (5) the mesotibial spurs equal to or shorter than the length of mesotarsomeres I–II (Fig. 13.9a). They are attractively colored dorsally (Fig. 13.22).

Classification. Relationships between this genus and other Laccophilinae are unknown. This genus was previously known only from three female specimens of *L. grouvellei* (Régimbart) (Brancucci, 1983a; Toledo *et al.*, 2003). The species was originally described in *Laccophilus* before being placed in its own genus by Brancucci (1983a). The genus may be closely related to the Neotropical *Laccodytes* (Toledo and Michat, 2015).



Map 13.8. Distribution of *Laccosternus*.

Diversity. The genus has two species, *L. grouvellei* and *L. krausi* Brancucci and Vongsana, and was revised recently (Brancucci and Vongsana, 2013).

Natural History. Little is known of the biology of this group. One specimen was found in a "consignment of tobacco," and another at light (Brancucci, 1983a). Brancucci and Vongsana (2013) speculated that *L. grouvellei*, though widespread, occurs in specialized habitats. *Lacconectus krausi* was collected in a small forest pond with numerous other diving beetle species (Brancucci and Vongsana, 2013).

Distribution. The species is found in Southeast Asia in Laos, Malaysia, Sumatra, and Vietnam (Map 13.8).

Fig. 13.23. *Napodytes boki*. Scale = 1.0mm.

Genus *Napodytes* Steiner, 1981

Body Length. 1.8mm.

Diagnosis. This is the only genus in the tribe characterized by a single apical tibial spur (Fig. 13.1).

Map 13.9. Distribution of *Napodytes*.

Napodytes antennae are sexually dimorphic with the male medial antennomeres expanded laterally (Figs. 13.2a,23) and the female antennae simple. These are small beetles (<1.8mm) (Fig. 13.23).

Classification. Steiner (1981) and Toledo *et al.* (2010) thought *Napodytes* is related to *Laccodytes*.

Diversity. The genus includes the single species, *N. boki* Steiner.

Natural History. Little is known of the biology of the group. The single species was described from one male and one female collected at light (Steiner, 1981). According to Steiner (1981), the beetles were able to jump like many of the laccophilines.

Distribution. The species is known only from the type locality in Ecuador (Map 13.9).

Genus *Neptosternus* Sharp, 1882

Body Length. 2.4–4.5mm.

Diagnosis. This group is easily diagnosable by the apically trifurcate prosternal process (Fig. 13.3a), which is unique among all diving beetles. The species also have the metatarsal lobes short compared to other laccophiline genera except *Philaccolus*. Many species are dorsally variously fasciate or maculate with some nearly entirely black (Fig. 13.24).

Classification. Toledo *et al.* (2010) thought that *Neptosternus* and the Neotropical *Laccodytes* may be closely related. They are resolved together with *Philaccolus* and *Philaccolilus* in the analysis by Ribera *et al.* (2008).

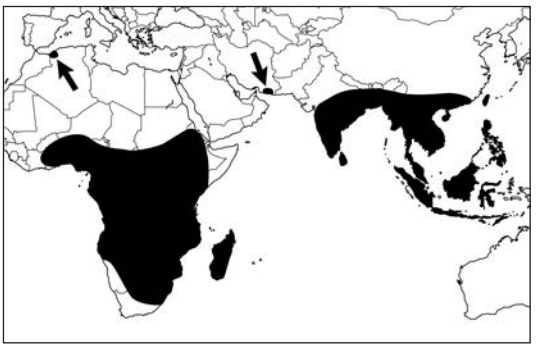
Diversity. There are currently 96 species in this large

Fig. 13.24. *Neptosternus* sp. Scale = 1.0mm.

group, which are extremely similar to each other externally. Taxonomic treatments of various regions include Africa (Guignot, 1959b; Omer-Cooper, 1970; Bilardo and Rocchi, 2012) and India, China and Southeast Asia (Vazirani, 1963; 1975; Holmen and Vazirani, 1990; Balke *et al.*, 1997a; Hendrich and Balke, 1997; 1999; 2000a; c; 2001b; 2003; Balke and Hendrich, 1998; 2001a; b; Zhao *et al.*, 2012).

Natural History. Nearly all species of *Neptosternus* are rheobiontic. They often come to lights.

Distribution. Species are found through the Afrotropical region across southern Asia and throughout Southeast Asia (Map 13.10).



Map 13.10. Distribution of *Neptosternus*.

Genus *Philaccolilus* Guignot, 1937

Body Length. 4.3–6.4mm.

Diagnosis. *Philaccolilus* are laccophilines with: (1) simple metatibial spurs (as in Fig. 13.4b); (2) a simple prosternal process; (3) the posteromedial margin of the pronotum relatively straight, not angulate (Fig. 13.25); (4) the elytral microreticulation with small, transverse cells (as in Fig. 13.10b); (5) the metacoxal lines slightly divergent anteriorly (Fig. 13.12c); (6) the metacoxal process apically with a single lobe (Fig. 13.12c); and (7) the metatarsal lobes relatively long (Fig. 13.13b). Unlike *Philaccolus*, members of the group lack a metacoxal/metafemoral stridulatory device (Fig. 13.12c). Specimens have the elytra black and variously marked with pale maculae, fasciae, and striae (Fig. 13.25).

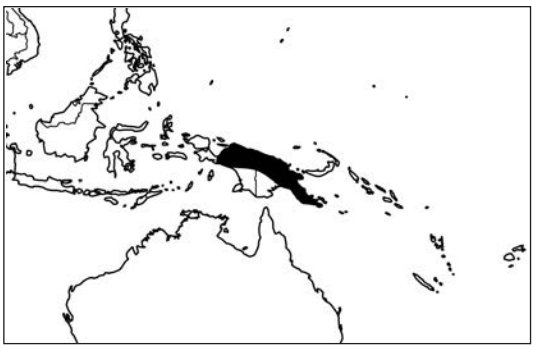
Fig. 13.25. *Philaccolilus bellissimus*. Scale = 1.0mm.

Classification. *Philaccolilus* was described as a subgenus of *Philaccolus* by Guignot (1937) but elevated to genus by Balke *et al.* (2000b). The group appears to be related to both *Neptosternus* and *Philaccolus* (Balke *et al.*, 2000b; Ribera *et al.*, 2008).

Diversity. There are currently 12 species recognized in *Philaccolilus*, most of them described recently in a revision by Balke *et al.* (2000b).

Natural History. All the known species are lotic in streams with a mineral, but not muddy, substrate (Balke *et al.*, 2000b).

Distribution. *Philaccolilus* are found in New Guinea (Map 13.11).



Map 13.11. Distribution of *Philaccolilus*.

Genus *Philaccolus* Guignot, 1937

Body Length. 3.0–4.0mm.

Diagnosis. *Philaccolus* are laccophilines with: (1) simple metatibial spurs (as in Fig. 13.4b); (2) a simple prosternal process; (3) the posteromedial margin of the pronotum relatively straight, not angulate (Fig. 13.26); (4) the elytral microreticulation with small, transverse cells (Fig. 13.10b); (5) the metacoxal lines distinctly divergent anteriorly (Fig. 13.12b); (6) the metacoxal process apically with a single lobe (Fig. 13.12b); and (7) the metatarsal

Fig. 13.26. *Philaccolus* sp. Scale = 1.0mm.

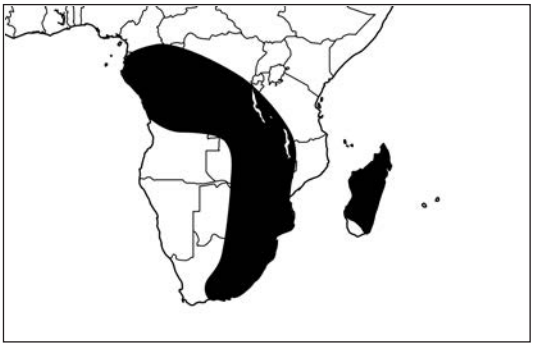
lobes relatively short (Fig. 13.13a). Members of the group have a stridulatory file on the surface of the metacoxa with the plectrum a sharpened ridge on the dorsal margin of the metafemur (Fig. 13.12b). This is similar to many *Laccophilus*, but the file is longer and more coarse in *Philaccolus* (Balke *et al.*, 2000b) and may not be homologous. Species typically are pale overall with dark elytra marked with many pale maculae (Fig. 13.26).

Classification. Little is known of *Philaccolus* relationships, though the genus is resolved as sister to *Neptosternus* + *Philaccolilus* in the analysis by Ribera *et al.* (2008). Balke *et al.* (2000b) thought the genus may be sister to *Neptosternus* based on both taxa having short metatarsal lobes (Fig. 13.13a).

Diversity. This poorly known taxon includes five species currently.

Natural History. These beetles are lotic and occur in rivers and small forest streams, though little has been described of their habitat.

Distribution. *Philaccolus* are found in Africa, including Madagascar (Map 13.12).



Map 13.12. Distribution of *Philaccolus*.

Fig. 13.27. *Philodytes umbrinus*. Scale = 1.0mm.

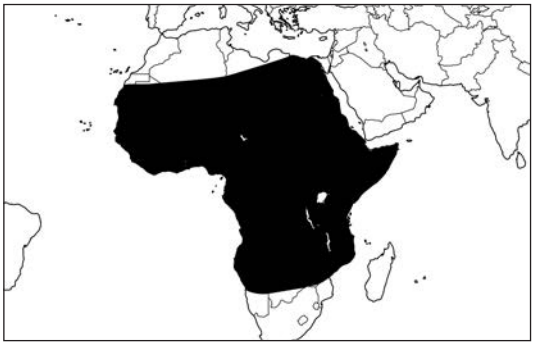
Genus *Philodytes* J. Balfour-Browne, 1939

Body Length. 5.2–6.0mm.

Diagnosis. Within the tribe, *Philodytes* can be distinguished by: (1) two metatibial spurs that are apically simple (Fig. 13.4b); (2) the prosternal process apically simple, narrow apically, and weakly carinate (Fig. 13.4b); (3) the base of the pronotum angulate medially (Figs. 13.5a,27); and (4) the pro- and mesofemora and tibiae not densely punctate (Fig. 13.6b).

Classification. This taxon was described first as a subgenus of *Laccophilus* (J. Balfour-Browne, 1939a) until elevated to genus rank by Guignot (1948a). Balke *et al.* (1997b) synonymized *Philodytes* with *Laccophilus,* suggesting that the simple metatarsal claws represent a reversal to the plesiomorphic state, but this has not been universally followed (Nilsson, 2001; Miller *et al.*, 2005).

Diversity. There is only a single species in the group, *Philodytes umbrinus* (Motschulsky).



Map 13.13. Distribution of *Philodytes*.

Natural History. *Philodytes umbrinus* occurs mainly in shallow lentic habitats, often temporary pools, sometimes with emergent vegetation but often with mineral substrates. The larval stage was described by Miller *et al.* (2005) using DNA sequence data to associate adults and larvae.

Distribution. *Philodytes* are mainly Afrotropical north to the Mediterranean in Egypt (Map 13.13).

14. Subfamily Cybistrinae

Body Length. 13.0–47.0mm.

Diagnosis. This subfamily is characterized by the following features: (1) apicoventral elytral setal patch small, composed of a field of short, coarse setae (Fig. 14.1a); (2) a large cluster of apically bifid setae on the posteroapical surface of the metatibia (Fig. 14.2a); and (3) the anteroapical metatibial spur acuminate and broader than the posteroapical spur (Fig. 14.2a). Male cybistrines have protarsomeres I–III broadly laterally expanded into a "palette" that is wider than its medial length with a large field of adhesive setae ventrally (Fig. 14.1b). Most members cybistrines are large to extremely large and are usually dark green to black, often with a lateral yellow margin along the pronotum and/or the elytra. Several synapomorphies of the female genitalia and larvae also make this group highly characteristic (Miller, 2001c; Miller *et al.*, 2007b; Alarie *et al.*, 2011a).

Classification. This well-defined group has always been considered monophyletic and associated with the subfamily Dytiscinae, though more comprehensive analyses have indicated that Dytiscinae, as historically defined, is not monophyletic (Ribera *et al.*, 2002b; 2008; Miller and Bergsten, 2014a), and the tribe was elevated to subfamily rank by Miller and Bergsten (2014a). Morphological characters supporting monophyly of Dytiscinae and cybistrines are, however, quite convincing. These include, in adults: (1) the anterior margins of the eyes rounded, not emarginate (see Fig. 15.1a,b); (2) the median lobe of the male aedeagus bilaterally symmetrical with a distinct, elongate ventral sclerite (see Fig. 15.1d); (3) females with a single genital opening in the female reproductive tract for both reception of sperm and oviposition (see Fig. 15.1e,f); and (4) the female gonocoxae fused together (see Fig. 15.1e,f).

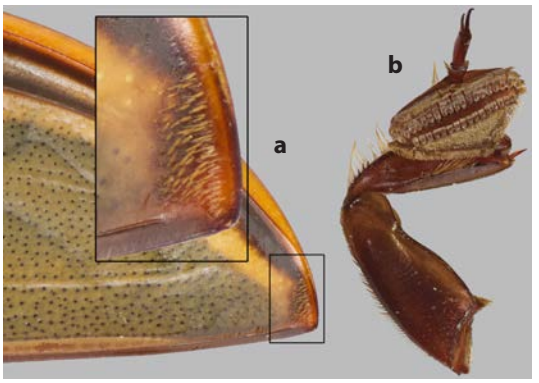


Fig. 14.1. Cybistrinae features. **a**, *Cybister gschwendtneri*, left elytral apex, ventral aspect. **b**, *C. fimbriolatus*, right male proleg, ventral aspect.

Larvae have: (1) abdominal segments VII–VIII with distinct lateral fringes of swimming setae (see Fig. 2.5h–j); and (2) the larval antennomeres and maxillary and labial palpomeres subsegmented (see Fig. 2.4b), among other things (Alarie *et al.*, 2011a). Nevertheless, the best recent phylogenetic analysis resulted in Cybistrinae sister to Laccophilinae and that clade sister to Dytiscinae (Miller and Bergsten, 2014a). If this gains greater support with the addition of more data, the convergence of character states between Cybistrinae and Dytiscinae (or their loss in Laccophilinae) will be a remarkable circumstance. Internal phylogenetic analysis and reclassification of Cybistrinae was done by Miller *et al.* (2007b). Several Australian genera and one African genus, *Regimbartina*, form a loosely associated group, and *Megadytes* and *Cybister*, the two largest genera, are sisters based on molecular data and morphological characters like the presence of a transverse groove across the metatrochanter (Fig. 14.2b).

Diversity. Cybistrinae includes seven genera with *Megadytes* and *Cybister*, the genera with the most species, each with several subgenera.

Natural History. These are among the largest of all diving beetles with members present mainly in large, lentic bodies of water. A few, such as *Austrodytes* species, are usually lotic. Some of the larger ones are well known to prey on small vertebrates.

Distribution. These beetles are found worldwide, but most members of the group are tropical with a few species occurring north to southern Canada and northern Europe. There are several species found in relatively temperate South America and Australia.

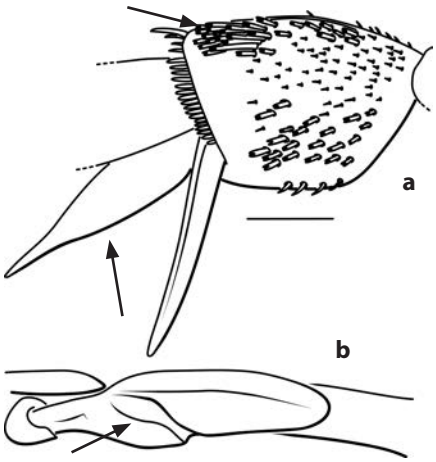


Fig. 14.2. Cybistrinae features. **a**, *Cybister gschwendtneri*, left metafemur, posterior aspect. **b**, *Megadytes robustus*, right metatrochanter, ventral aspect. Scale = 1.0mm.

Key to the Genera of Cybistrinae

1 Posterior metatibial spur bi- or trifurcate (Fig. 14.3a,b); Neotropical (Map 14.3) . . . . . *Megadytes* (in part), 107

1' Posterior metatibial spur simple (Fig. 14.3c) 2

2(1) Prosternal process with prominent longitudinal sulcus (Fig. 14.4a,b) 3

2' Prosternal process without prominent longitudinal sulcus though lateral margins may be variously bordered and anterior portion may be shallowly sulcate (Fig. 14.4c,d) 4

3(2) Metacoxal lines absent (Fig. 14.5a); northern Australia, New Guinea, and the Moluccas (Map 14.7) . . . . . *Sternhydrus*, 110

3' Metaxocal lines present (see Fig. 14.5b); south Australia (Map 14.6) . . . . *Spencerhydrus*, 109

4(2) Metacoxal lines absent (as in Fig. 14.5a); southern Australia and New Zealand (Map 14.4) . . . . . *Onychohydrus*, 108

4' Metacoxal lines present (Fig. 14.5b) 5

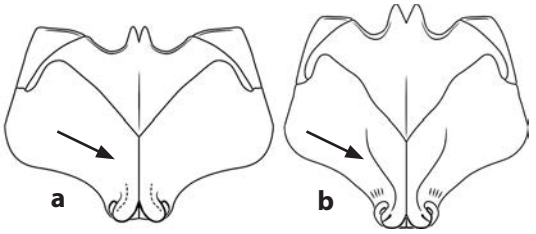


Fig. 14.5. Cybistrini, metaventrite and metacoxae. **a**, *Sternhydrus atratus*. **b**, *Cybister fimbriolatus*

5(4) Male with one metatarsal claw (Fig. 14.6a,b), female either with one claw (Fig. 14.6a) or with an additional, small posterior claw (Fig. 14.6b); with posteroventral series of setae near apical margin of mesotarsomeres of males and pro- and mesotarsomeres of females (Fig. 14.7a); male sternite VIII with medial margin emarginate (Fig. 14.8a); circumtropical north into Nearctic and Palearctic regions (Map 14.2) . . . . . *Cybister*, 106

5' Male and female with two metatarsal claws, though female may have posterior claw rudimentary (Fig. 14.6c); without posteroventral series of setae on pro- and mesotarsomeres (Fig. 14.7b); male sternite VIII medially with margin straight (Fig. 14.8b) 6

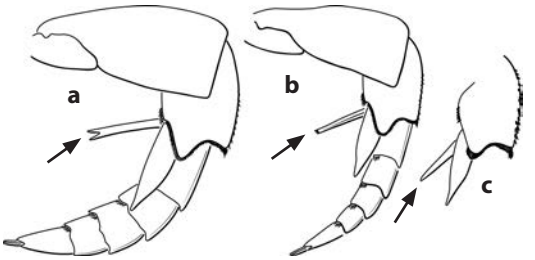


Fig. 14.3. Cybistrini left metalegs. **a**, *Megadytes* (*Bifurcitus*) *lherminieri*. **b**, *M.* (*Trifurcitus*) *robustus*. **c**, *Cybister tripunctatus*.

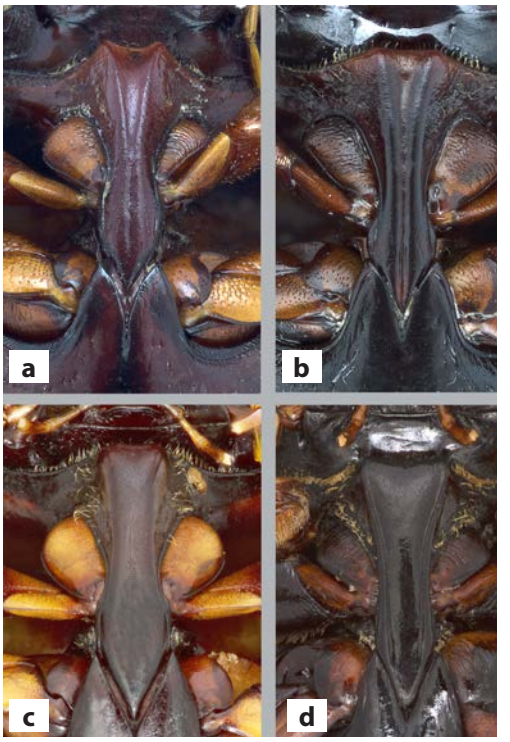


Fig. 14.4. Cybistrini, prosternal processes. **a**, *Sternhydrus atratus*. **b**, *Spencerhydrus pulchellus*. **c**, *Cybister tripunctatus*. **d**, *Austrodytes insularis*.

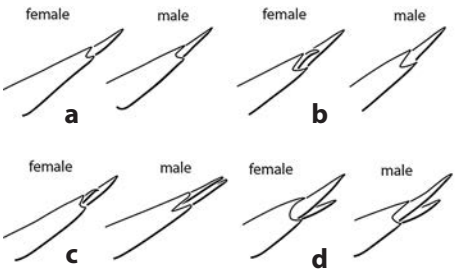


Fig. 14.6. Cybistrini, metatarsal claws. **a**, *Cybister gschwendtneri*. **b**, *C. marginicollis*. **c**, *Megadytes fraternus*, **d**. *Austrodytes insularis*.

6(5) Male with two metatarsal claws subequal in length, female with two metatarsal claws but with posterior claw shorter (Fig. 14.6c); Neotropical and southern Nearctic (Map 14.3) . . . . . *Megadytes* (in part), 107

6' Male and female with claws similar, anterior claw shorter than posterior (Fig. 14.6d) . . . 7

7(6) Dorsal surface light green with sparsely distributed, small black spots (Fig. 14.14); lateral margins of prosternal process without distinct carinae (Fig. 14.9a); central Afrotropical (Map 14.5). . . . . *Regimbartina*, 109

7' Dorsal surface dark green without black spots (Fig. 14.10); lateral margins of prosternal process with distinct lateral carinae (Fig. 14.9b); north Australia (Map 14.1). . *Austrodytes*, 105

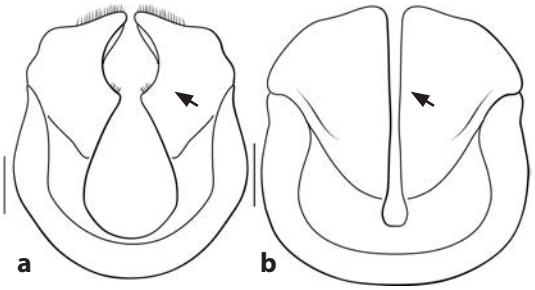


Fig. 14.8. Cybistrini, male ventrite VIII. **a**, *Cybister tripunctatus*. **b**, *Megadytes fraternus*. Scales = 1.0mm.

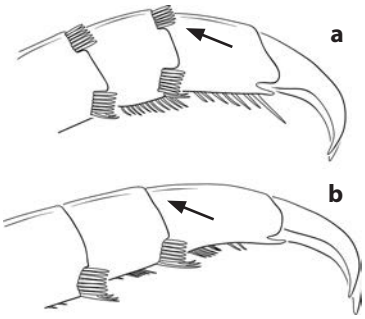


Fig. 14.7. Cybistrini, mesotarsomeres, posterior aspect. **a**, *Cybister tripunctatus*. **b**, *Megadytes fraternus*.

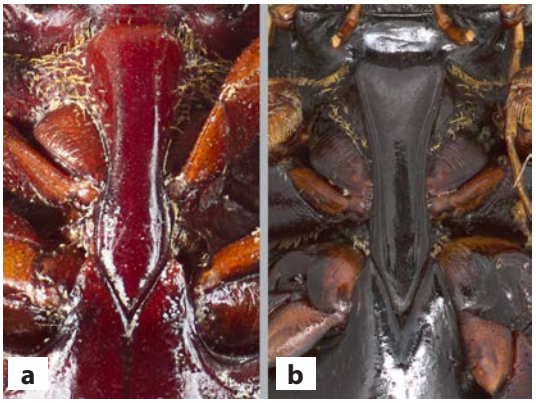


Fig. 14.9. Cybistrini, prosternal processes. **a**, *Regimbartina pruinosa*. **b**, *Austrodytes insularis*.

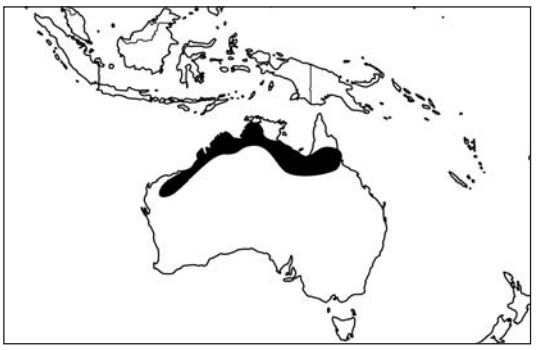
Fig. 14.10. *Austrodytes insularis*. Scale = 1.0mm.

Genus *Austrodytes* Watts, 1978

Body Length. 18.0–20.0mm.

Diagnosis. These cybistrines have the lateral margins of the prosternal process distinctly carinate (Fig. 14.9b), the male and female metatarsal claws similar with the anterior claw shorter than the posterior (Fig. 14.6d), and the metacoxal lines distinctly present (as in Fig. 14.5b). *Austrodytes* are also characterized by being relatively flattened (Fig. 14.10) and having both large and small punctures on the elytron. These are medium-sized cybistrines that are dark green with pale lateral margins on the elytra and pronotum (Fig. 14.10).

Classification. The genus is part of a clade including three other Australian taxa, *Spencerhydrus*, *Onychohydrus*, and *Sternhydrus* (Miller *et al.*, 2007b).



Map 14.1. Distribution of *Austrodytes*.

Diversity. There are currently two species in this genus, *A. insularis* (Hope) and the more recently described *A. plateni* Hendrich, identifiable using characters presented by Hendrich (2003).

Natural History. *Austrodytes* occur in cold, clear, permanent streams in hills (Hendrich, 2003).

Distribution. The two species are known from northern and northwestern Australia (Map 14.1).

Genus *Cybister* Curtis, 1827

Body Length. 13.0–43.0mm.

Diagnosis. Within Cybistrinae, the genus *Cybister*, though diverse and speciose, is well characterized by several distinct synapomorphies, including: (1) a series of setae present along the posteroventral apical margin of the mesotarsomeres of males and pro- and mesotarsomeres of females (Fig. 14.7a); (2) males with a single metatarsal claw, females with one or two, and if two, then the posterior claw small (Fig. 14.6a,b); and (3) the medial margin of the lobes of the male abdominal sternum VIII emarginate (Fig. 14.8a). Species are medium in size to among the largest of any dytiscids. They range from green to black, and many have distinctive pale lateral margins on the elytra and pronotum (Fig. 14.11a,b,d) though others are uniformly dark dorsally (Fig. 14.11c).

Classification. As a group, *Cybister* is sister to *Megadytes*. This large and diverse genus has a history of subgeneric subdivisions, such as those established by Brinck (1945). This classification was criticized and revised by Miller *et al.* (2007b), who recognized four subgenera based on monophyletic groups resulting from a comprehensive cladistic analysis. *Cybister* (*Megadytoides*) Brinck includes species with yellow on the lateral margin of the pronotum, but not laterally on the elytron (Fig. 14.11a), and males with a single metatarsal claw and females with two claws, the posterior claw small. *Cybister* (*Melanectes*) Brinck are *Cybister* without distinctive yellow or pale margins on the elytron or pronotum (Fig. 14.11c) and males with a single metatarsal claw, and females with two claws, the posterior claw small. *Cybister* (*Neocybister*) Miller *et al.* are species with distinctive lateral yellow margins on the pronotum and elytra (Fig. 14.11b) and males with a single metatarsal claw, females with two claws, the posterior claw sinuate and small. Finally, *Cybister s. str.* have distinctive yellow margins laterally on the pronotum and elytron (Fig. 14.11d) and males with a single metatarsal claw and females variable, most with a single claw, but a few North and Central American species have females with either one claw or also an additional small posterior claw.

Diversity. There are currently 96 species in the genus, with most of the species in *Cybister s. str.* and *C.* (*Melanectes*). There are no comprehensive revisions, but Nearctic species can be identified using Miller (2013b), African species by Guignot (1961), Indian species by Vazirani (1968), Australian by Watts (1978), the Palearctic by Zaitzev (1953), and some of the Neotropical by Trémouilles and Bachmann (1980).

Natural History. These are among the largest invertebrate predators in many aquatic systems around the world. *Cybister* are typically in lentic habitats, often with considerable vegetation, but can be found in slower lotic areas. Certain North American members of *Cybister* have males with an apparent stridulatory device formed from a series of ridges at the base of the metacoxa and the posterior margin of the trochanter (Fig. 14.5b, Larson and Pritchard, 1974),

Fig. 14.11. *Cybister* species. **a**, *C.* (*Megadytoides*) *marginicollis*. **b**, *C.* (*Neocybister*) *puncticollis*. **c**, *C.* (*Melanectes*) *sugillatus*. **d**, *C.* (*C.*) *tripunctatus*. Scales = 1.0mm.

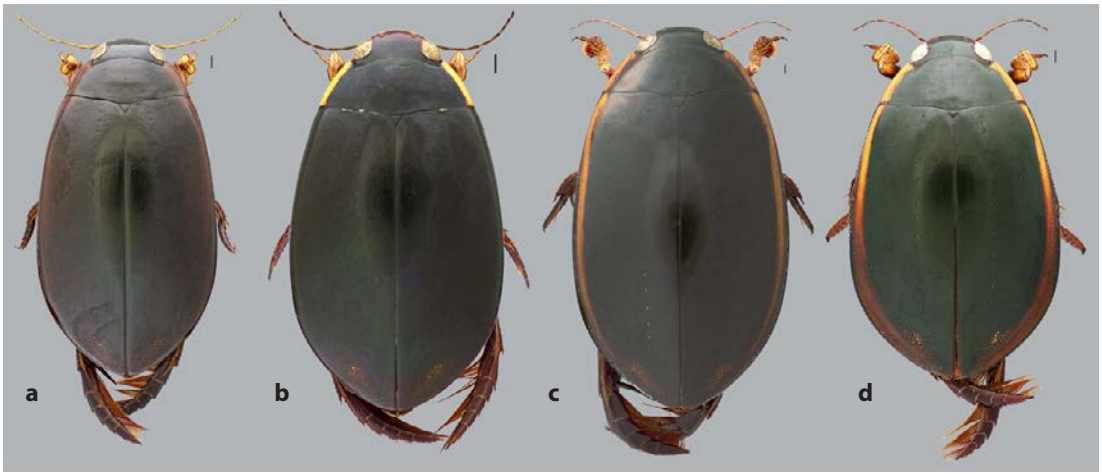
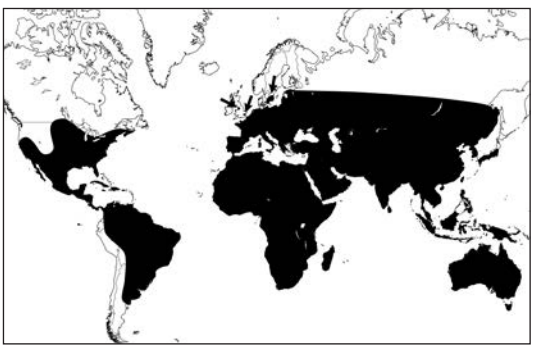


Fig. 14.12. *Megadytes* species. **a**, *M.* (*Paramegadytes*) *glaucus*. **b**, *M.* (*M.*) *carcharias*. **c**, *M.* (*Bifurcitus*) *lherminieri*. **d**, *M.* (*Trifurcitus*) *robustus*. Scales = 1.0mm.

though, to date, no one has characterized any sound produced by this device. It seems likely to be used in sexual signaling since it is only found on males and does not appear to be used defensively (such as when handled). Given how common and abundant they are and their large size, it is unsurprising that there has been considerable biology and natural history investigation of *Cybister*. There are a number of papers on their physiology (Voïnov, 1902; Mukerji, 1930; Ranade, 1969; Kallapur, 1970a; b; 1973; 1978; Shrivastava, 1971; Johnson, 1972a; Rao, 1972; Meyer-Rochow, 1973; Kallapur and Narsubhai, 1974; 1976a; b; Kallapur *et al.*, 1976; Ciofi Luzzatto and Leoni, 1978; Barde, 1981; Mukherjee *et al.*, 1989; Sen *et al.*, 1993; Assar and Younes, 1994; Dilshad Begum and Dharani, 1996; Roy, 2000; Zhou *et al.*, 2006; Shahab *et al.*, 2011), internal anatomy (Sidhu, 1961; Mathur and Goel, 1966; Kallapur, 1970a; Behura *et al.*, 1975; Khan *et al.*, 1996; Kumar *et al.*, 2000; 2001; Kumar and Ehteshamuddin, 2002; Wei *et al.*, 2003), chemistry (Meinwald *et al.*, 1998), development (Khalil and Farahat, 1968a; b; 1969b; Urbani, 1970; Shirgur, 1975; Panov, 2014), nutrition and feeding habits (Khalil and Farahat, 1969a; Johnson and Jakinovich, 1970; Ideker, 1979; Bose and Sen, 1981; Guo *et al.*, 2003), and behavior and ecology (Fiori, 1949; Vazirani, 1964b; Khalil and Farahat, 1968b; Johnson, 1972b; Roy and Sinha, 2002; Onoda, 2004; Inoda, 2011a). Immature stages were described by several authors (Wilson, 1923; Vazirani, 1964b; Watts, 1965; Galewski, 1973b).



Map 14.2. Distribution of *Cybister*.

Distribution. Members of *Cybister* are found in all major biogeographic regions (Map 14.2), though they are most speciose and abundant in tropical latitudes. Although a distinct fauna is present in both the Holarctic and Neotropical regions, the group is not diverse in either of these where it is largely replaced by *Dytiscus* (Holarctic) and *Megadytes* (Neotropical). The group reaches its greatest diversity in the Afrotropical and Oriental regions.

Genus *Megadytes* Sharp, 1882

Body Length. 16.5–47.0mm.

Diagnosis. Members of this genus are similar to *Cybister* but differ from other members of the subfamily in having males with two equal-length metatarsal claws and females with two claws, but with the posterior claw shorter than the anterior (Fig. 14.6c). Some members of the group (*M.* (*Trifurcitus*) Brinck and especially *M.* (*Bifurcitus*) Brinck) are among the largest diving beetles with the lateral margins of the pronotum and elytra margined with yellow (Fig. 14.12c,d) and with the posterior metatibial spur either bifid or trifid (Figs. 14.3a,b). Others (*Megadytes s. str.* and *M.* (*Paramegadytes*) Trémouilles and Bachmann) are large, but smaller than the other sub-

genera and have the lateral yellow margin absent on the elytron and sometimes vague or nearly absent on the pronotum as well (Fig. 14.12a,b).

Classification. *Megadytes* has four subgenera that together are monophyletic (Miller *et al.*, 2007b). *Megadytes* and *Cybister* are sister groups (Miller *et al.*, 2007b) and are similar in many respects. *Megadytes s. str.* includes 10 species. Although medium sized to large (15–24mm), these are relatively smaller than members of the other subgenera, and the group has few obvious synapomorphies. Its members lack distinctive lateral yellow margins on the elytra, but typically have yellow margins on the pronotum (Fig. 14.12b). *Megadytes* (*Bifurcitus*) includes the largest diving beetles with three species that are characterized by the apically bifid posterior metibial spurs (Fig. 14.3a) and distinctive lateral yellow margins on the pronotum and elytra (Fig. 14.12c). *Megadytes* (*Trifurcitus*) includes six species that are similar to *M*. (*Bifurcitus*) in their large size and lateral yellow margins on the pronotum and elytra (Fig. 14.12d), but the posterior metatibial spurs are apically trifid (Fig. 14.3b). The last subgenus, *M*. (*Paramegadytes*), has two species that are relatively large, but without lateral yellow margins (Fig. 14.12a) and with simple metatibial spurs.

Diversity. There are altogether 21 species in 4 subgenera in *Megadytes*. Most of them (but not all) were revised by Trémouilles and Bachmann (1980).

Natural History. *Megadytes* are characteristic of heavily vegetated, permanent lentic water bodies, where they often occur in deeper areas than many other diving beetles. They come to lights. This group includes the largest species of diving beetles, *M*. (*Bifurcitus*) *lherminieri* (Guérin-Méneville), *M*. (*B*.) *ducalis* Sharp, and *M*. (*B*.) *magnus* Trémouilles and Bachmann, which are up to 50mm in length as adults with both adults and larvae capable of eating large prey items, such as anuran larvae and other vertebrates. Other members of *Megadytes* are also known to feed on vertebrate prey. Immature stages of several species have been described (Cekalovic-Kuschevich, 1974; Crespo, 1982; Ferreira, 1993; 1995; 2000; Michat, 2006a).

Distribution. This is a Neotropical group with members as far north as southern Florida, USA, and the Bahamas south through the Caribbean and Central America and throughout lowland South America (Map 14.3).

Map 14.3. Distribution of *Megadytes*.

Genus *Onychohydrus* Schaum and White, 1847

Body Length. 24.0–28.0mm.

Diagnosis. Within Cybistrinae this genus has the following character combination: (1) male and female metatarsal claws similar and the anterior claw shorter than the posterior (as in Fig. 14.6d); (2) the prosternum and prosternal process not longitudinally sulcate; and (3) the metacoxal lines absent (as in Fig. 14.5a). Specimens are large and dorsally green with yellow lateral margins on the pronotum and elytron (Fig. 14.13).

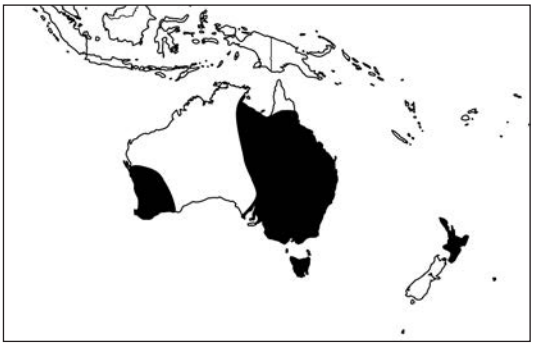
Classification. This group was historically placed together with *Sternhydrus* in one genus, but Miller *et al.* (2007b) elevated *Sternhydrus* to genus rank (see below). The genus is part of a clade including the other Australian cybistrine genera, *Spencerhydrus*, *Austrodytes*, and *Sternhydrus* (Miller *et al.*, 2007b).

Diversity. There are two species currently placed in the genus, *O. scutellaris* (Germar) and *O. hookeri* (White). The genus was treated by Watts (1978) and Ordish (1966) under the name *Homoeodytes*.

Fig. 14.13. *Onychohydrus scutelleris*. Scale = 1.0mm.

Natural History. Specimens can often be collected in heavily vegetated lentic situations. Larvae of the Australian species were described by Watts (1965).

Distribution. *Onychohydrus scutellaris* occurs in southwestern and eastern Australia and Tasmania (Map 14.4) and possibly New Zealand, though its presence there is based on a single, dubious record (Ordish, 1966). *Onychohydrus hookeri* does occur on New Zealand's North Island (Map 14.4).



Map 14.4. Distribution of *Onychohydrus*.

Genus *Regimbartina* Chatanay, 1911

Body Length. 19.0–23.0mm.

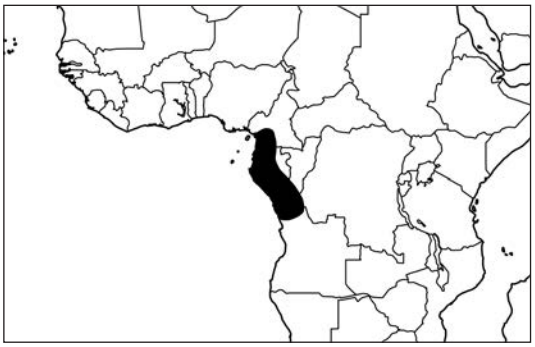
Diagnosis. The single species in this genus exhibits mainly plesiomorphic features, in general, and lacks the attributes that characterize the other cybistrine genera. The genus is diagnosed by the following: (1) males and females have similar metatarsal claws with the anterior claw shorter than the posterior (as in Fig. 14.6d); (2) the prosternal process is not longitudinally grooved or laterally beaded or carinate (Fig. 14.9a); and (3) the dorsal surface is light green with sparsely distributed, small black spots (Fig. 14.14). Specimens are robust and large.

Classification. *Regimbartina* is a rarely collected taxon, and little is known of its relationship with other members of the Cybistrini. It was not included in the phylogenetic analysis by Miller *et al*. (2007b).

Diversity. There is a single, poorly known species in this group, *R. pruinosa* (Régimbart).

Natural History. Nothing is known about the natural history of the single, rare species in the genus.

Distribution. *Regimbartina* are found in Cameroon, Angola, and Gabon (Map 14.5).



Map 14.5. Distribution of *Regimbartina*.

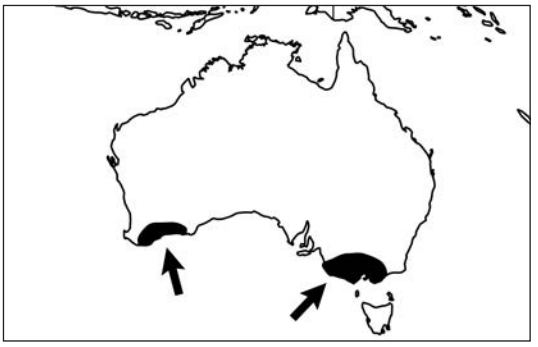
Genus *Spencerhydrus* Sharp, 1882

Body Length. 17.0–18.0mm.

Diagnosis. This genus is characterized by mainly

Fig. 14.14. *Regimbartina pruinosa*. Scale = 1.0mm.

Fig. 14.15. *Spencerhydrus latecinctus*. Scale = 1.0mm.



Map 14.6. Distribution of *Spencerhydrus*.

plesiomorphies within Cybistrinae, though it does have a few unique features. *Spencerhydrus* have the prosternum and prosternal process longitudinally deeply grooved (Fig. 14.4b) combined with distinct metacoxal lines (as in Fig. 14.5b). They are relatively small for the subfamily and are dorsally dark green with lateral yellow margins on the pronotum and elytron (Fig. 14.15).

Classification. *Spencerhydrus* is sister to *Onychohydrus*, *Sternhydrus,* and *Austrodytes.*

Diversity. There are two species in this genus, *S. latecinctus* Sharp and *S. pulchellus* Sharp, which can be identified using a key by Watts (1978).

Natural History. Specimens of *Spencerhydrus* have been collected in lentic habitats with considerable emergent vegetation. They are relatively uncommon, and little is known of their biology.

Distribution. The two species are found in southern Australia, *S. latecinctus* from the southeast and *S. pulchellus* from the southwest (Map 14.6).

Genus *Sternhydrus* Brinck, 1945

Body Length. 15.5–20.0mm (possibly 25.5mm).

Diagnosis. Even though members of this group are characterized by numerous plesiomorphies within Cybistrinae, the genus has a number of unique features as well. *Sternhydrus* are diagnosed by: (1) a distinctly longitudinally sulcate prosternum and prosternal process, at least anteriorly (Fig. 14.4a); (2) the metacoxal lines absent or indistinct (Fig. 14.5a); and (3) males and females with similar metatarsal claws with the anterior claw shorter than the posterior (Fig. 14.6d). Specimens are moderately large and dorsally green with yellow lateral margins on the pronotum and elytron (Fig. 14.16), except *S. kolbei* (Wilke), which lacks yellow margins.

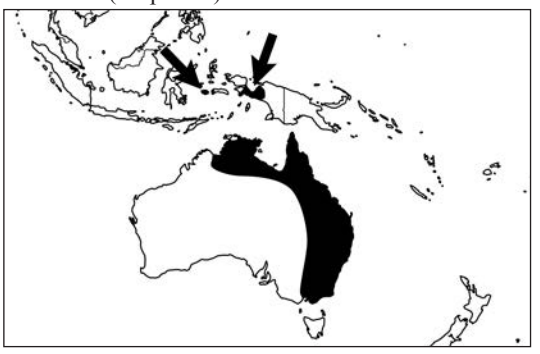
Fig. 14.16. *Sternhydrus atratus.* Scale = 1.0mm.

Classification. *Sternhydrus* was historically recognized as a subgenus of *Onychohydrus* (Brinck, 1945; Watts, 1978) based in large part on the absence of distinct metacoxal lines in both groups. However, Miller *et al.* (2007b) elevated the group to genus rank. *Sternhydrus* are distinctive compared with *Onychohydrus,* which, although also without metacoxal lines, also lack the longitudinally sulcate prosternum and prosternal process of *Sternhydrus*, which are more similar to *Spencerhydrus*. It is part of a clade including other Australian taxa, *Spencerhydrus*, *Onychohydrus*, and *Austrodytes* (Miller *et al.*, 2007b).

Diversity. There are four species, one Australian, *S. atratus* (Fabricius), and three from New Guinea and Moluccas in this poorly known genus. The species *S. kolbei* (Wilke) is larger (24.0–25.5mm), lacks yellow lateral margins, and was doubtfully placed in *Sternhydrus* by Brinck (1945).

Natural History. Members of this group are found mainly in well-vegetated lentic situations. Larvae of *S. atratus* were described by Watts (1965).

Distribution. Found in northern and eastern Australia, western New Guinea, and Buru Island of the Moluccas (Map 14.7).



Map 14.7. Distribution of *Sternhydrus*.

15. Subfamily Dytiscinae

Body Length. 6.5–44.0mm.

Diagnosis. These are Dytiscidae with: (1) the eyes anteriorly rounded, not emarginate along the anterolateral margin (Fig. 15.1a,b); (2) the aedeagus (both the median lobe and lateral lobes) bilaterally symmetrical (Fig. 15.1d); (3) females with a single genital opening for sperm reception and ovipositing (Fig. 15.1e,f; Burmeister, 1976; Miller, 2001c); (4) the gonocoxae of the ovipositor fused dorsally (Fig. 15.1e,f; Burmeister, 1976; Miller, 2001c); (5) the prosternum and prosternal process together in the same plane (Fig. 15.1c); (6) the pro- and mesotarsi distinctly pentamerous (Fig. 15.2); and (7) males with the protarsal adhesive setae apically each with a circular sucker disc and with the shaft centrally inserted on the disc (Fig. 15.2a; females without adhesive setae, Fig. 15.2b). These beetles are medium sized to very large. The scutellum is externally visible with the elytra closed (Fig. 15.4b) except in Aubehydrini (Fig. 15.4a). Protarsomeres I–III of males are together broadly expanded, forming a large, rounded "palette" with ventral adhesive setae (Fig. 15.2a). Dytiscinae has historically included those taxa placed here in Cybistrinae, and they share a number of synapomorphies in both adults and larvae (Alarie *et al.*, 2011a; Miller and Bergsten, 2014a). Adult diagnostic differences between the groups include the round sucker discs in males of

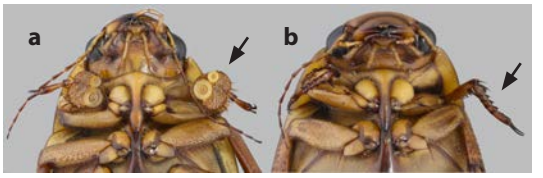


Fig. 15.2. *Dytiscus marginalis*, ventral surface. **a**, Male. **b**, Female.

Dytiscinae (Fig. 15.2a) compared with elongate oval or long, flattened sucker discs in males of Cybistrinae (see Figs 2.11i,14.1b), and the anterior metatibial spur expanded and apically acuminate in Cybistrinae (see Fig. 14.2a), but both spurs are similar in size and both are slender in Dytiscinae (Fig. 15.3).

Classification. This group has maintained its taxon composition for a long time with a couple of exceptions. The tribe Cybistrini has been only occasionally recognized at the subfamily rank (e.g., Michael and Matta, 1977), but recent evidence (Ribera *et al.*, 2008; Miller and Bergsten, 2014a) has indicated the group is not related to other Dytiscinae, and Miller and Bergsten (2014a) formally removed the clade from Dytiscinae and placed it at the subfamily rank (see under Cybistrinae). The other significant exception is the species *Notaticus fasciatus* Zimmermann, which was originally described in Hydaticini. Guignot (1949) subsequently described the junior synonym *Aubehydrus speciosissimus* Guignot and

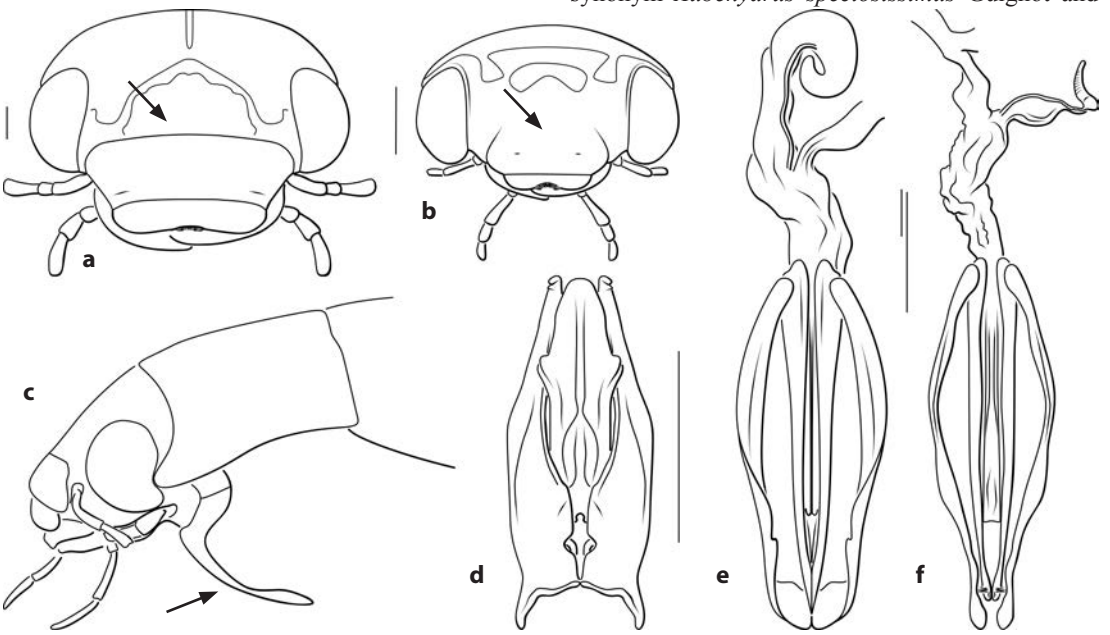


Fig. 15.1. Dytiscinae features. **a**, *Dytiscus verticalis* head, anterior aspect. **b**, *Acilius abbreviatus* head, anterior aspect. **c**, *D. marginalis* lateral aspect. **d**, *Thermonectus basillaris* male genitalia, dorsal aspect. **e**, *D. verticalis* female genitalia, ventral aspect. **f**, *Hydaticus dorsiger* female genitalia, ventral aspect. Scales = 1.0mm.

placed it in its own subfamily Aubehydrinae Guignot based in large part on the absence of an externally visible scutellum. Miller (2000) found evidence for placement of the species within Dytiscinae and revised the classification, which was also confirmed with larval features (Miller *et al.*, 2007a; Alarie *et al.,* 2011a) and other analyses (Ribera *et al.*, 2002b; 2008; Miller and Bergsten, 2014a).

Diversity. Dytiscinae includes five tribes and altogether twelve genera.

Natural History. These are among the largest of all diving beetles. They are characteristic of ponds and lakes with extensive marginal vegetation, though they can be found in various habitats. Many of the largest species have been implicated in predation on vertebrates, to the extent that some may occasionally be pests in fish-farming operations (Wilson, 1923; Bisht and Das, 1979a; 1985; Adeyemo *et al.*, 1997).

Distribution. There are groups of Dytiscinae in each biogeographic region, with major groups endemic to certain regions. They are well represented in temperate climates and high elevations to lowland tropical habitats.

Key to the Tribes of Dytiscinae

1 Apices of both metatibial spurs bifid (Fig. 15.3e); series of bifid setae on posterior surface of metatibia oblique (Fig. 15.3e) . . . . . Aciliini, 125

1' Apices of both metatibial spurs simple (Fig. 15.3a–d); series of bifid setae on posterior surface of metatibia oblique, linear, or curved (Fig. 15.3a–d) 2

2(1) Scutellum not externally visible with elytra closed (Fig. 15.4a). Neotropical (see Map 18.1). . . . . Aubehydrini, 121

2' Scutellum visible externally with elytra closed (Fig. 15.4b) 3

3(2) Anterolateral margin of metasternal wing straight (Fig. 15.5a); most species with dorsal surfaces of protibia and protarsi of male with stridulatory apparatus (Fig. 15.6); female with sides of pronotum and base of elytron often with complex, irregular, incised grooves (Fig. 15.7a). . . . . Hydaticini, 118

3' Anterolateral margin of metasternal wing distinctly convexly curved (Fig. 15.5b); protibial stridulatory apparatus absent; female without dorsal modifications or with entire pronotum and elytron covered with dense, conspicuous rugosity (Fig. 15.7b) or elytron with longitudinal grooves (Fig. 15.7c). 4

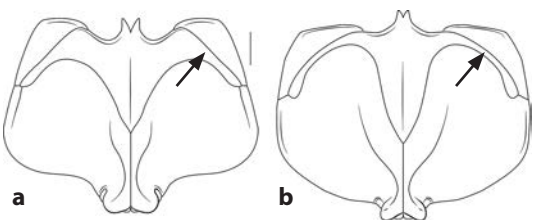


Fig. 15.5. Dytiscinae metacoxae and metaventrites. **a**, *Hydaticus aruspex*. **b**, *Eretes sticticus*. Scales = 1.0mm.

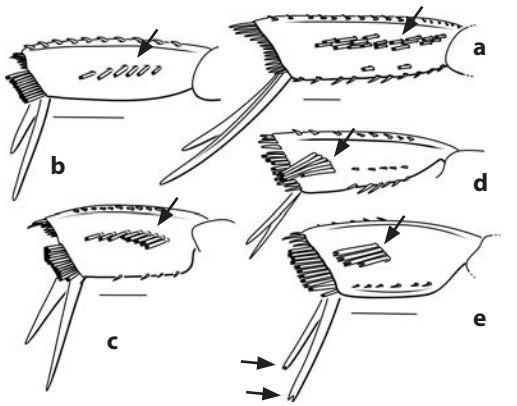


Fig. 15.3. Dytiscinae metatibiae, posterior aspect. **a**, *Dytiscus verticalis*. **b**, *Hydaticus aruspex*. **c**, *Hydaticus flavolineatus*. **d**, *Eretes sticticus*. **e**, *Acilius abbreviatus*. Scales = 1.0mm.

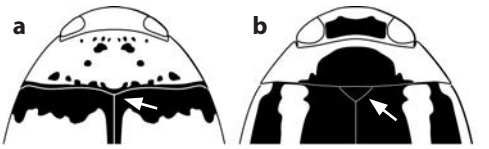


Fig. 15.4. Hydaticini dorsal aspect. **a**, *Notaticus fasciatus*. **b**, *Hydaticus bivittatus*.

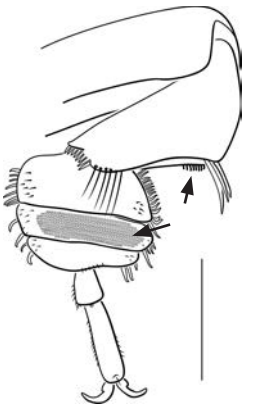


Fig. 15.6. *Hydaticus aruspex* proleg. Scale = 1.0mm.

4(3) Lateral pronotal margin narrowly beaded (Fig. 15.8a); posterolateral margin of elytron with series of short, acute spines (Fig. 15.9a); female pronotum and elytron not conspicuously modified; body length 10–19mm . . . . . Eretini, 123

4' Lateral pronotal margin broadly beaded (Fig. 15.8b) or without bead (Fig. 15.8c); posterolateral margin of elytron without short spines (Fig. 15.9b); some female specimens (not all) with pronotum and elytron covered with dense, conspicuous rugosity (Fig. 15.7b) or deep, longitudinal grooves (Fig. 15.7c); body length 19–44mm . . . . . .Dytiscini, 114

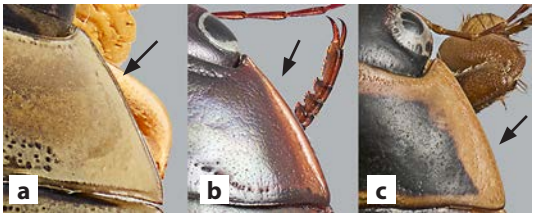


Fig. 15.8. Dytiscinae right pronotal margins. **a**, *Eretes griseus*. **b**, *Hyderodes shuckardi*. **c**, *Dytiscus marginalis*.

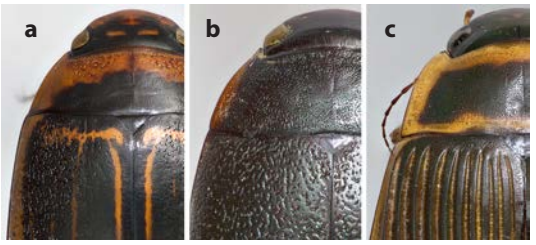


Fig. 15.7. Dytiscinae female dorsal surfaces. **a**, *Hydaticus continentalis*. **b**, *Hyderodes shuckardi*. **c**, *Dytiscus marginalis*.

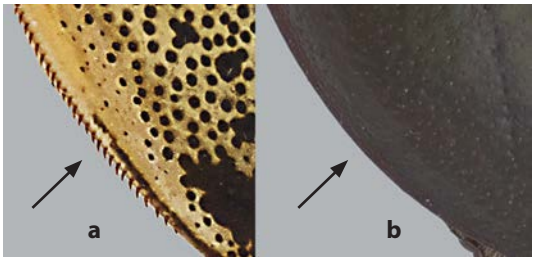


Fig. 15.9. Dytiscinae left apicolateral elytral margins. **a**, *Eretes griseus*. **b**, *Hyderodes shuckardi*.

16. Tribe Dytiscini

Body Length. 19.0–44.0mm.

Diagnosis. Members of this group have simple metatibial spurs that are similar in size (Fig. 16.1a), the scutellum externally visible with the elytra closed (Figs. 16.6,7), the anterolateral margin of the metasternal wing convex (Fig. 16.1), and the lateral margin of the pronotum either unbeaded (Fig. 16.3a) or with a broad bead (Fig. 16.3b). These are large, conspicuous beetles. Each genus is distinctive, but there are really no convincing morphological synapomorphies for the group. They are mainly characterized by the absence of features unique to other members of the subfamily. Because of their large size, these species, especially *Dytiscus*, can be potentially confused with Cybistrinae, but specimens are easily separated from that subfamily by, among other things, the different shape of the metatibial spurs. These are similar in size and shape in Dytiscini (Fig. 16.1a), whereas the anterior spur in Cybistrinae is broad and acuminate (see Fig. 14.2a).

Classification. Sharp (1882) included *Hyderodes* and *Dytiscus* together in a group, a taxonomy that was generally followed (e.g., Roughley, 1990). However, Hyderodini was erected by Miller (2000) for *Hyderodes* based on evidence that that genus is sister to a clade including Aubehydrini, Hydaticini, Eretini, and Aciliini, and is not sister to *Dytiscus*. Subsequent analyses also indicated that *Hyderodes* and *Dytiscus* are not related (Miller, 2001c; Ribera *et al.*, 2002b; 2008). However, the most recent comprehensive analysis by Miller and Bergsten (2014a) placed *Hyderodes* and *Dytiscus* together, and the traditional classification of Dytiscini was restored.

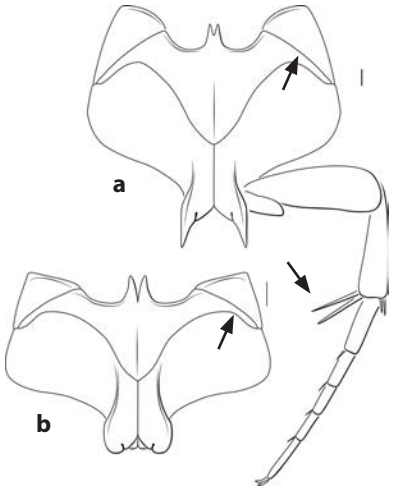


Fig. 16.1. Dytiscini metacoxae and metaventrites. **a**, *Dytiscus lapponicus,* including left metaleg. **b**, *Hyderodes shuckardi*. Scales = 1.0mm.

Diversity. The tribe includes two genera, *Dytiscus* and *Hyderodes*.

Natural History. These are large to very large species. Both genera are usually found in lentic bodies of water, often with extensive vegetation, though they can be found in the margins of rivers and streams also.

Distribution. Dytiscini has a disjunct distribution with *Hyderodes* found in temperate southern Australia and *Dytiscus* found across the Holarctic region.

Key to the Genera of Dytiscini

1 Frontoclypeal margin entire (Fig. 16.2a); pronotum without lateral bead (Fig. 16.3a); male with two large and many small protarsal adhesive setae, large setae with fringe of fine setae (Fig. 16.4a); some female specimens of some species (not all) with deep, closely spaced longitudinal grooves on elytron (Fig. 16.6b,d); dorsal surface of median lobe of aedeagus with two rows of long, fine setae (Fig. 16.5a); Holarctic (Map 16.1) . . . . . *Dytiscus*, 115

1′ Frontoclypeal margin broadly interrupted medially (Fig. 16.2b); pronotum with broad lateral bead (Fig. 16.3b); male with protarsal setae similar in size, without fringe of fine setae (Fig. 16.4b); some female specimens (not all) with dorsal surface covered with complex

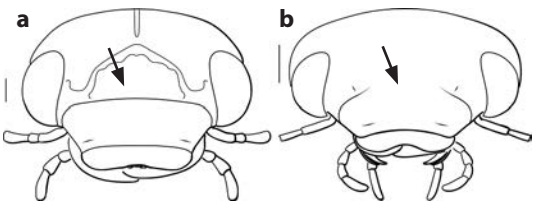


Fig. 16.2. Dytiscini heads, anterior aspect. **a**, *Dytiscus verticalis*. **b**, *Hyderodes shuckardi*. Scales = 1.0mm.

granulations (Fig. 16.7c); dorsal surface of median lobe of aedeagus without rows of long, fine setae, though short spines may be present (Fig. 16.5b); Australia (Map 16.2)
. . . . . *Hyderodes*, 117

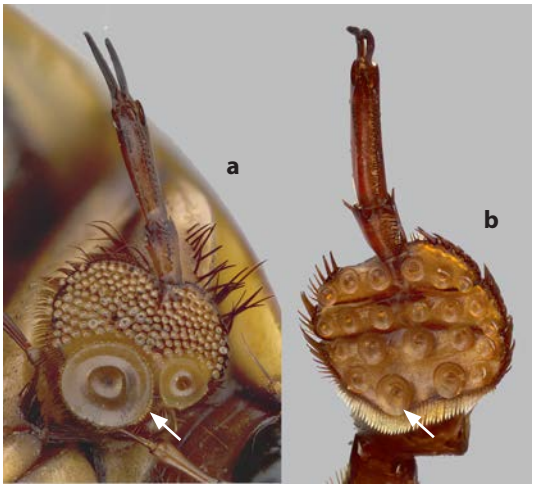


Fig. 16.4. Dytiscini male protarsi ventral aspect. **a**, *Dytiscus fasciventris*. **b**, *Hyderodes shuckardi.*

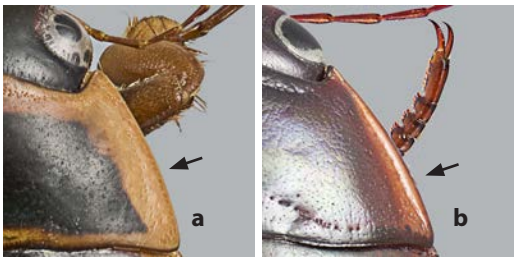


Fig. 16.3. Dytiscini lateral pronotal margin. **a**, *Dytiscus marginalis*. **b**, *Hyderodes shuckardi.*

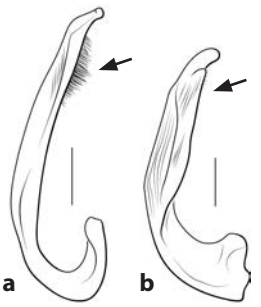


Fig. 16.5. Dytiscini median lobes, right lateral aspect. **a**, *Dytiscus dauricus*. **b**, *Hyderodes shuckardi.* Scales = 1.0mm.

Genus *Dytiscus* Linnaeus, 1758

Body Length. 22.0–44.0mm.

Diagnosis. These are among the largest species of diving beetles, equaled in size only by cybistrines. Large size and lateral margins of yellow on the pronotum and elytron make these beetles distinct from most other dytiscids except members of Cybistrinae and a few large species of Hydaticini, from which *Dytiscus* can be further distinguished by having: (1) a complete frontoclypeal suture (Fig. 16.2a); (2) relatively elongate and slender metathoracic legs (Fig. 16.1a); (3) female specimens of many species with deep longitudinal sulci on the elytra (Fig. 16.6b,d); (4) the adhesive setae of the male protarsi round and sucker-shaped and of two sizes, two very large ones and a field of smaller ones (Fig. 16.4a); (5) the large adhesive setae with a marginal fringe of multibranched setae (Fig. 16.4a); and (6) the male median lobe with a dorsal series of setae (Fig. 16.5a).

Classification. *Dytiscus* was one of the first 25 Coleoptera genera erected by Linnaeus (1758), though at the time it included other groups of aquatic beetles. The current definition of the genus dates to Erichson (1832), and the phylogeny was examined by Roughley (1990) and Bergsten (1999).

Diversity. There are currently 27 recognized species and 4 subspecies in the group that can be identified using the revision by Roughley (1990).

Natural History. *Dytiscus* occur in a variety of habitats but are usually in lentic water bodies with heavy vegetation. They may also be found in pools in slow streams, beaver ponds, forest pools, bogs, etc. Possibly because of their large size and chemical defenses, they occur in ponds with fish more commonly than other dytiscids. They are predators of small fish, anuran larvae, and even snakes (e.g., Drummond and Wolfe, 1981). The natural history, classification, and morphology of *D. marginalis* is among the best studied of any beetle, in part because of work leading to the publication of a two-volume opus edited by Korschelt (1923; 1924).

The unusual longitudinal grooves present on the elytra in some females of many species (Fig. 16.6b,d) and the large, circular adhesive discs on the protarsi of males (Fig. 16.4a) were once thought to cooperatively assist both males and females with mating activities (Darwin, 1859). Only recently have they been implicated in a sexual antagonism model of sexual evolution in the group (Bergsten, 1999; Bergsten *et al.*, 2001; Miller, 2003; Miller and Bergsten, 2014b). The proportion of females with elytral grooves varies between populations and between species, and the mode of selection maintaining dimorphic populations has been studied (Härdling and Bergsten, 2006; Karlsson Green *et al.*, 2013).

Unsurprisingly, given their conspicuous-

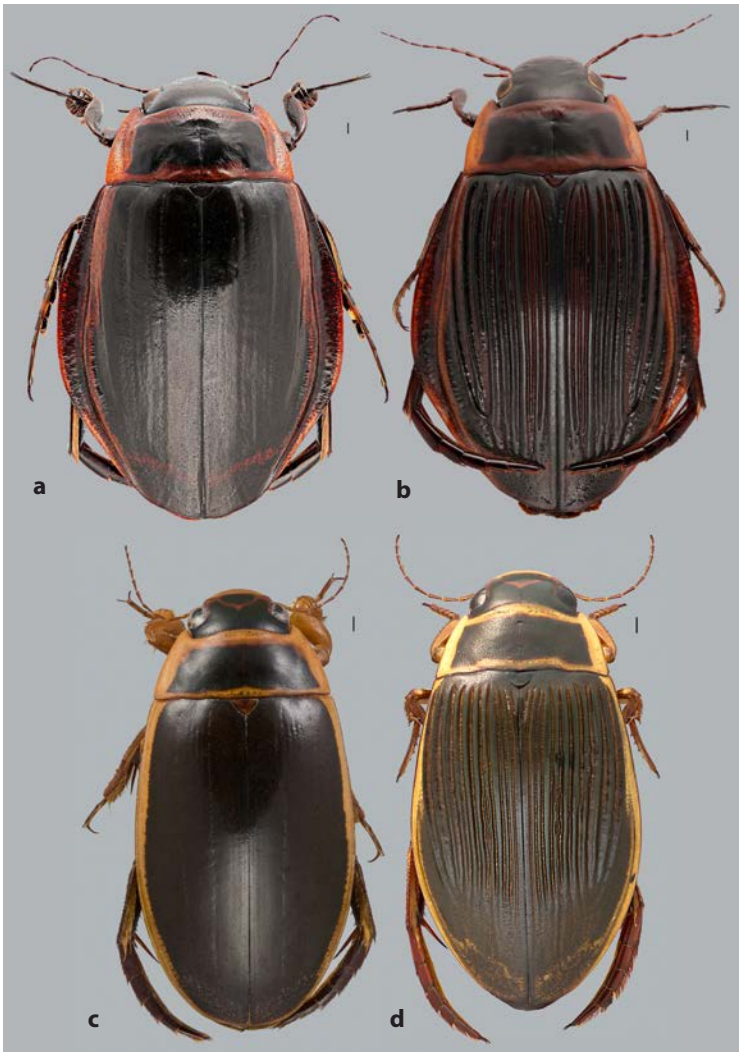
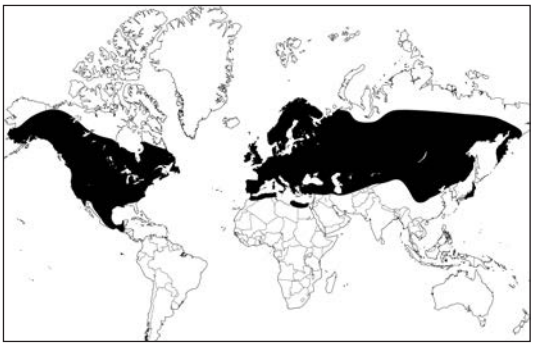


Fig. 16.6. *Dytiscus* species. **a**, *D. latissimus*, male. **b**, *D. latissimus*, female. **c**, *D. marginalis*, male. **d**, *D. marginalis*, female.

ness in Europe and North America, there are an exceptional number of papers on the natural history of members of this group, including papers on their chemistry, physiology, and genetics (Auerbach, 1893; Abraham, 1962; 1965a; b; 1966a; b; 1967a; b; 1969; 1976; Schildknecht and Hotz, 1967; Horridge, 1969; Steinert and Urbani, 1969; Grillot, 1970; Horridge *et al.*, 1970; Urbani, 1970; 1973; Autuori *et al.*, 1971; Nagl, 1973; Mackie and Walker, 1974; Trendelenburg, 1974; Nachtigall and Bilo, 1975; Schmitz and Komnick, 1976; Trendelenburg *et al.*, 1976; Werner, 1976a; b; Scheer and Zentgraf, 1978; Andries, 1983; Roychoudhury and Raghuvarman, 1986; Frisbie, 1988; Frisbie and Dunson, 1988a; b; Yadav *et al.*, 1988; Verma and Baluni, 1990; Di Giovanni *et al.*, 1999; Shakuntala, 2002); development (Bier and Ribber, 1966; Kuhn *et al.*, 1972; Bauer, 1986); internal morphology (Andersen and Beams, 1957; Galassi, 1974); parasites (Aiken, 1985); and ecology, evolution, and behavior (Régimbart, 1877; Jackson, 1957; 1958a; 1959; 1960a; Hughes, 1958; Buck, 1966; Reddy *et al.*, 1967; Young, 1967b; Nelson, 1977; Brodie and Formanowicz, 1981; Drummond and Wolfe, 1981; Formanowicz and Brodie, 1981; Formanowicz, 1982; 1987; Pelham-Clinton, 1982; Barker, 1984; Leclair *et al.*, 1984; Aiken and Wilkinson, 1985; Bauer and Gewecke, 1985; Gewecke, 1985; Holomuzki, 1985a; b; 1988; Aiken, 1986a; b; 1992; Leclair *et al.*, 1986; Schneider, 1986; Braasch, 1989; Aiken and Khan, 1992; Johansson and Nilsson, 1992; Litt, 1992; Bergsten, 1999; Inoda and Tsuzuki, 1999; Inoda *et al.*, 2000; Bergsten *et al.*, 2001; Inoda, 2001; 2003; 2011a; b; Laurila *et al.*, 2001; Inoda *et al.*, 2004; 2007; Vahrushev, 2011). Larvae of numerous species have been described (Wilson, 1923; James,

1969; Watts, 1970; Barman, 1972; Galewski, 1973b; White and Barman, 2000; Kamite, 2003).

Distribution. This is a Holarctic genus with one species extending through Mexico to Central America in the Nearctic and to northern Africa and south-central China in the Palearctic (Map 16.1). Two species are Holarctic. *Dytiscus semisulcatus* O. F. Müller has at least once been found on New Zealand, most likely introduced (Ordish, 1966).

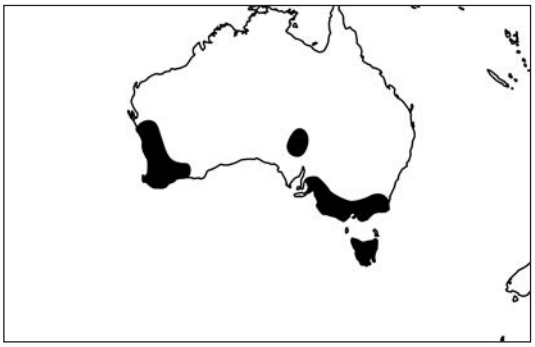


Map 16.1. Distribution of *Dytiscus*.

Genus *Hyderodes* Hope, 1838

Body Length. 19.0–21.0mm.

Diagnosis. This genus is characterized by the following character combination: (1) the lateral margin of the pronotum is broadly beaded (Fig. 16.3b); (2) the metatibial spurs are similar in size and shape and apically simple (as in Fig. 16.1a); (3) the frontoclypeal suture is discontinuous medially (Fig. 16.2b); (4) some female specimens are dorsally covered with irregular, rugose sculpturing on the pronotum and elytron (Fig. 16.7c), though not all are modified (Fig. 16.7b); and (5) the male median lobe has dorsal short, stout, spinous setae (Fig. 16.5b).



Map 16.2. Distribution of *Hyderodes*.

Classification. Based on the most recent analysis (Miller and Bergsten, 2014a), *Hyderodes* is sister to *Dytiscus*, an unusual sister-group relationship between a Holarctic and an Australian clade.

Diversity. Only two similar species are known, *H. crassus* Sharp and *H. shuckardi* Hope. They can be identified using a key presented by Watts (1978).

Natural History. Specimens can be found in marshes and ponds with dense vegetation. The dramatically rugose dorsal sculpturing in some female specimens (Fig. 16.7c) may be a sexual antagonism response to the large male suction discs on the protarsi (Fig. 16.4b) used to grasp females before and during mating (Miller, 2003; Miller and Bergsten, 2014b). Larvae have been described by Watts (1965).

Distribution. There are two southern Australian species, *H. crassus* from the southwest and *H. shuckardi* from the southeast including Tasmania (Map 16.2).

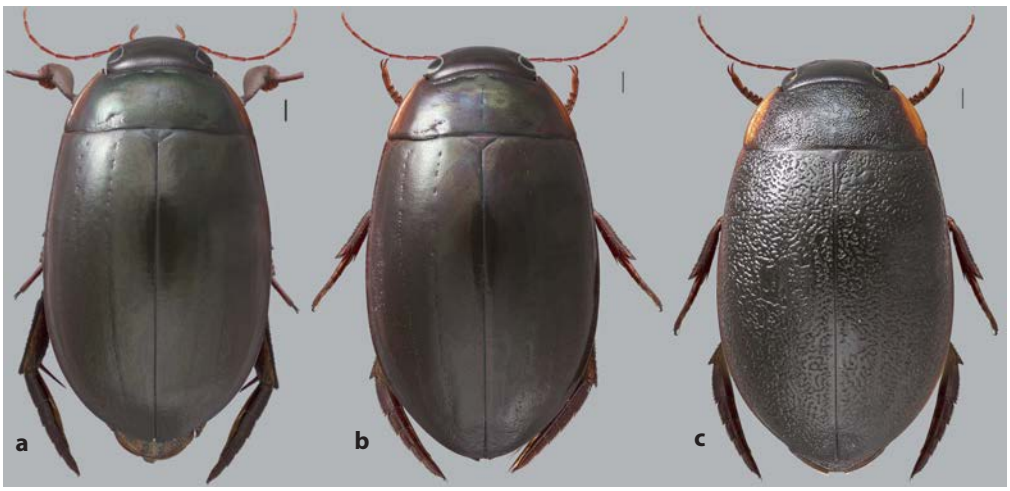


Fig. 16.7. *Hyderodes shuckardi*. **a**, Male. **b**, Nongranulate female. **c**, Granulate female.

17. Tribe Hydaticini

Body Length. 8.5–20.5mm.

Diagnosis. This group is characterized within the subfamily by two distinct features: (1) the anterolateral margin of the metaventrite (anterior margin of the metasternal wing) is straight or slightly concave (Fig. 17.1a), and (2) males have a stridulatory apparatus formed by a reticulate file on the dorsal surface of male protarsomere II and short spines on the dorsoapical margin of the protibia (Fig. 17.1b, Larson and Pritchard, 1974; Miller, 2003, absent in a few species). Also, females have rugose sculpturing to a varying degree on the pronotum and elytron from nearly absent to covering much of the surface (Fig. 17.2). These are medium to large diving beetles.

Classification. Hydaticini belong to a clade that includes Aciliini, Eretini, and Aubehydrini, based in part on the common presence of series of golden setae along the posterior margins of metatarsomeres I–IV (Fig. 17.3). Historically, Hydaticini has included two genera, *Prodaticus* Sharp and *Hydaticus* Leach, the latter with several subgenera, including *Hydaticus s. str.*, *H.* (*Guignotities*) Brinck, *H.* (*Hydaticinus*) Guignot, and *H.* (*Pleurodytes*) Régimbart. A recent cladistic analysis by Miller *et al.* (2009a) resulted in a revised classification that recognized the same two genera, but with dramatic content rearrangement. *Prodaticus*, which previously included only two species, was synonymized with each of the *Hydaticus* subgenera except *Hydaticus s. str.* Thus the content of the genus *Hydaticus* was reduced to only 7 species, whereas *Prodaticus* included about 130, but with each group more convincingly monophyletic. This arrangement was rejected by Nilsson (2010), who preferred to preserve taxon content stability by recognizing a single genus with two subgenera, *Hydaticus s. str.* and *H.* (*Prodaticus*), the arrangement we also use here. *Notaticus* (Aubehydrini) was originally included in Hydaticini, but several recent analyses have indicated they are not together monophyletic (Miller, 2000; 2001c; Ribera *et al.*, 2008; Miller and Bergsten, 2014a; but see Ribera *et al.*, 2002b).

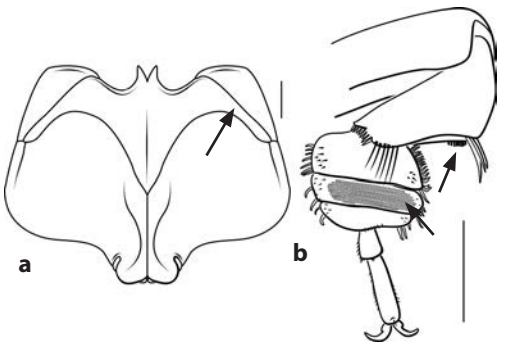


Fig. 17.1. Hydaticini features. **a**, *Hydaticus aruspex*, metaventrite and metacoxae. **b**, *H. aruspex*, male proleg and stridulatory device. Scales = 1.0mm.

Fig. 17.2. *Hydaticus continentalis* female left dorsal surface.

Diversity. The tribe consists of the single genus *Hydaticus*, with two subgenera.

Natural History. Hydaticines are medium to large beetles in mainly lentic habitats. They are often conspicuous and occur in large numbers. This group has some interesting sexually dimorphic features, including irregular rugosity of the dorsal surface of the pronotum and/or elytron in females, which may be a sexual conflict response to the large sucker disc adhesive setae on the expanded male protarsomeres I–III (Miller, 2003; Miller and Bergsten, 2014b). Males of most species have an apparent stridulatory device (see Fig. 16.1b, Larson and Pritchard, 1974; Miller *et al.*, 2009a; Miller and Bergsten, 2014b), which suggests sexual acoustic signaling since it does not appear to be used defensively. To date, no one has published evidence of the sound produced.

Distribution. As a group, the tribe occurs worldwide with certain subgroups restricted to particular regions. A great many species are tropical, though there are groups in temperate latitudes as well.

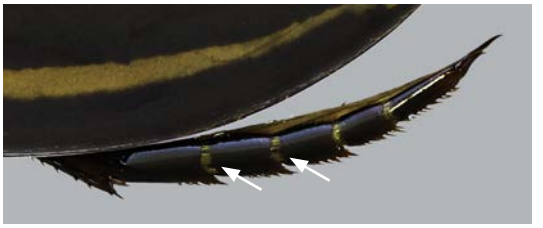


Fig. 17.3. *Hydaticus quadrivittatus* left metatarsus.

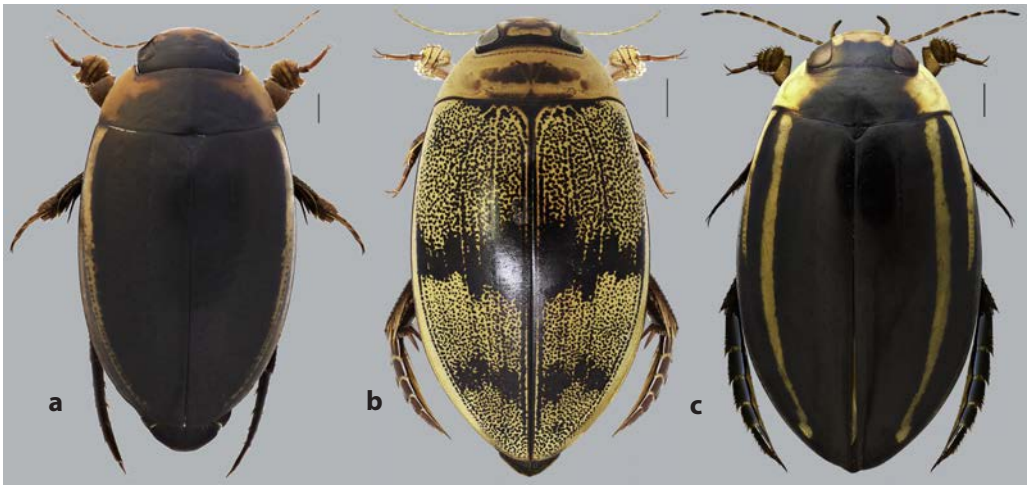


Fig. 17.4. *Hydaticus* species. **a**, *H.* (*H.*) *seminiger*. **b**, *H.* (*P.*) *matruelis*. **c**, *H.* (*P.*) *quadrivittatus*. Scales = 1.0mm.

Genus *Hydaticus* Leach, 1817

Diagnosis. This is the only genus in the tribe, and it is characterized by its diagnosis. These are large to quite large, often attractively marked beetles (Fig. 17.4)

Classification. Two subgenera are currently recognized (see above under Hydaticini). *Hydaticus s. str.* are hydaticines with the anterior surfaces of the metafemur and metatibia with fine punctation (Fig. 17.5a), a series of bifid setae on the posterior surface of the metatibia in a linear series approximately parallel to the dorsal margin of the metatibia (Fig. 17.5b), the basal setal patch on male mesotarsomere I large, forming a broad brush (Fig. 17.5e), and the fused female gonocoxae apically sharply acute and knife-like (Fig. 17.5g). *Hydaticus* (*Prodaticus*) have the anterior surfaces of the metafemur and metatibia without fine punctation, the series of bifid setae on the posterior surface of the metatibia curved ventrad proximally (Fig. 17.5d, except in the Neotropical *H.* (*P.*) *xanthomelas* Brullé (Fig. 17.5c) and the Palaearctic *H.* (*P.*) *pictus* (Sharp) and *H.* (*P.*) *africanus* Rocchi which have this series in a nearly straight line), the basal brush of setae on male mesotarsomere I small and linear (Fig. 17.5f), and the female gonocoxae apically relatively broad (Fig. 17.5h), not strongly knife-like as in *Hydaticus s. str*.

Diversity. There are 143 recognized species in *Hydaticus*. *Hydaticus s. str.* includes 7 known species

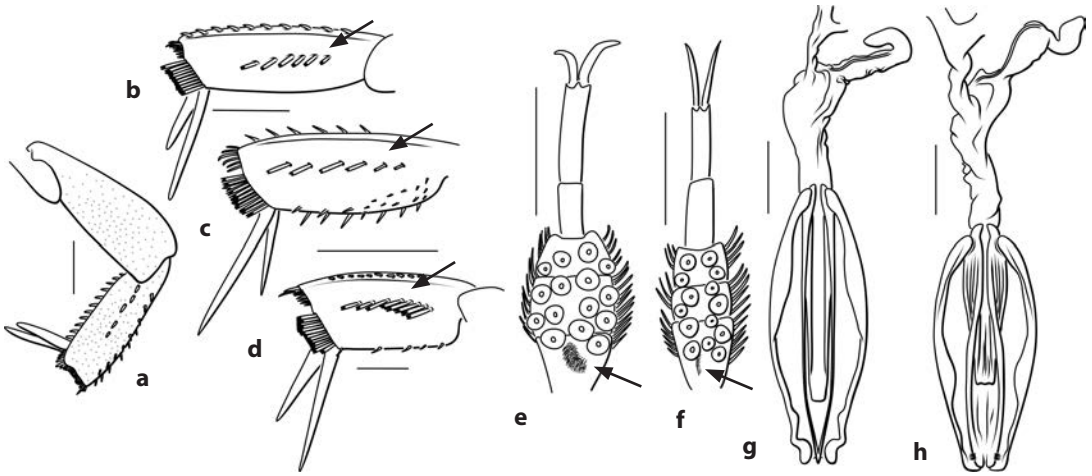
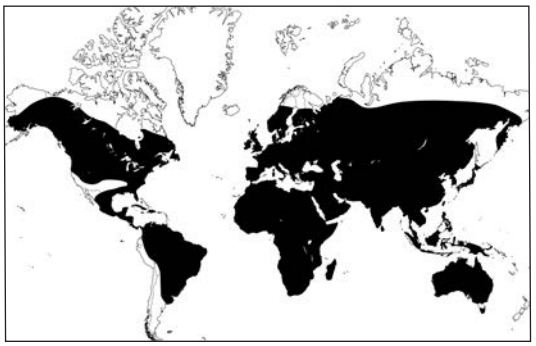


Fig. 17.5. Hydaticini features. **a**, *Hydaticus* (*H.*) *aruspex*, metathoracic leg, anterior aspect. **b**, *H.* (*H.*) *aruspex* metatibia, posterior aspect. **c**, *H.* (*P.*) *xanthomelas* metatibia, posterior aspect. **d**, *H.* (*P.*) *flavolineatus* metatibia, posterior aspect. **e**, *H.* (*H.*) *aruspex* mesotarsus, ventral aspect. **f**, *H.* (*P.*) *luczonicus* mesotarsus, ventral aspect. **g**, *H.* (*H.*) *aruspex* female genitalia, ventral aspect. **h**, *H.* (*P.*) *flavolineatus* female genitalia, ventral aspect. Scales = 1.0mm.

that can be identified using papers by Zimmermann and Gschwendtner (1937), Roughley and Pengelly (1981), Nilsson (1981; 1996b), Nilsson and Holmen (1995), and Larson *et al.* (2000). *Hydaticus* (*Prodaticus*) historically included only 2 species, *P. pictus* and *P. africanus*, but with the reclassification by Miller *et al.* (2009a), the group now includes 136 species worldwide. There are no recent comprehensive species-level revisions, but important species group or regional works include Guignot (1961), Satô (1961), Wewalka (1975; 1979; 2015), Watts (1978), Roughley and Pengelley (1981), and Trémouilles (1994). Miller *et al.* (2009a), among others (e.g., Guignot, 1961; Satô, 1961; Wewalka, 1975; 1979), have informally recognized a number of distinctive species groups within the subgenus *H.* (*Prodaticus*).

Natural History. *Hydaticus* are characteristic of lentic waters, including bogs and fens and other cool- or cold-water habitats (*Hydaticus s. str*.) or marshes, ponds, forest pools, etc. (*H*. (*Prodaticus*)). They often come to lights. Larvae were described by Galewski (1973b; 1975; 1981a; 1985; 1990b).

Distribution. Collectively the group occurs worldwide with *Hydaticus s. str.* found in the Holarctic region and *H*. (*Prodaticus*) primarily found at low latitudes, with a few extending into temperate latitudes (Map 17.1).



Map 17.1. Distribution of *Hydaticus*.

18. Tribe Aubehydrini

Body Length. 6.5–10.0mm.

Diagnosis. Within Dytiscinae, members of this tribe are unique in having a concealed scutellum (Fig. 18.3). *Notaticus* are relatively small and elongate (Fig. 18.3) compared with other dytiscines and have the prosternal process apically relatively broad (Fig. 18.1). They have series of golden setae along the apical margins of metatarsomeres I–IV characteristic also of Eretini, Hydaticini, and Aciliini (Fig 18.2). Dorsally they are dark with a prominent transverse pale macula across the elytral base (Fig. 18.3).

Classification. *Notaticus* was originally described in Hydaticini by Zimmermann (1928). Guignot (1942) erected a new subfamily, Aubehydrinae Guignot, for his new genus, *Aubehydrus* Guignot, but his genus name was later synonymized with *Notaticus* by Spangler (1973b), though it remained in its own subfamily until Miller (2000) convincingly placed it back within Dytiscinae. This was further confirmed in other phylogenetic analyses (Miller, 2001c; Ribera *et al.*, 2002b; 2008; Miller *et al.*, 2007a; Alarie *et al.*, 2011a; Miller and Bergsten, 2014a). The proposed relationships of *Notaticus* with other dytiscinaes are somewhat less clear, as sister to Hydaticini + Eretini + Aciliini (Miller, 2000; 2001c), sister to Aciliini (Miller, 2003), within Hydaticini (Ribera *et al.*, 2002b), as sister to (Aciliini + Eretini) + (Hyderodini + Hydaticini) (Ribera *et al.*, 2008), or as sister to Aciliini + Eretini (Miller and Bergsten, 2014a).

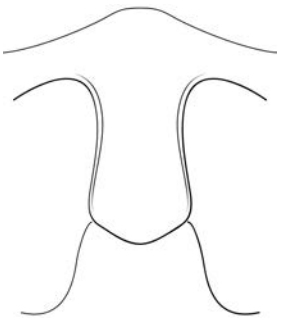


Fig. 18.1. *Notaticus fasciatus* prosternal process.

Fig. 18.2. *Notaticus fasciatus* left metatarsus.

Diversity. *Notaticus* is the only genus in this tribe.

Natural History. See below under *Notaticus*.

Distribution. See below under *Notaticus*.

Genus *Notaticus* Zimmermann, 1928

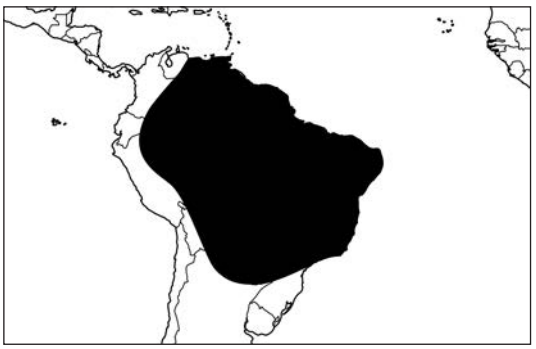
Diagnosis. This is the only genus in the tribe and is characterized by its diagnostic features (see above).

Fig. 18.3. *Notaticus fasciatus*. Scale = 1.0mm.

Classification. See above under Aubehydrini.

Diversity. Two species are currently placed in *Notaticus*, *N. fasciatus* Zimmermann and a recently described species from Venezuela, *N. obscurus* García and Navarro. The type of *N. obscurus* (in the Universidad Central de Venezuela, Maracay, Venezuela) was examined by Miller (unpublished), and the two species are likely synonyms.

Natural History. Members of the species have been



Map 18.1. Distribution of *Notaticus*.

collected from lowland tropical ponds and marshes. They occasionally come to lights. They are relatively rare and are not often collected in series. Spangler (1973b) provided information about biology of the species. Miller *et al.* (2007a) described the larva.

Distribution. *Notaticus* are widespread in lowland Neotropical areas from Venezuela south to southern Bolivia (Map 18.1).

19. Tribe Eretini

Body Length. 10.5–19.0mm.

Diagnosis. The only genus in the tribe, *Eretes*, is quite distinctive within the Dytiscinae and is characterized by adults with: (1) the prosternal process apically narrow and sharply pointed (Fig. 19.1); (2) the pronotum with a narrow lateral marginal bead (Fig. 19.2a); (3) the surfaces of the meso- and metatarsomeres with adpressed, flattened setae (Fig. 19.3); (4) the posterolateral margin of the elytron with a linear series of short, curved, black spines (Fig. 19.2b); (5) the elytra very thin and flattened and relatively lightly sclerotized overall (Fig. 19.4); (6) the elytra punctate with each puncture bearing a black spot (Fig. 19.4); and (7) otherwise pale coloration on all surfaces with small to extensive black markings on the dorsum of the head, pronotum, and elytra (Fig. 19.4).

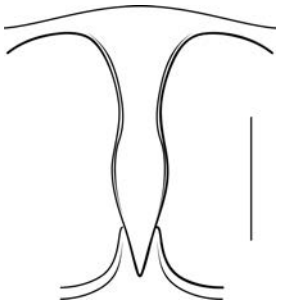


Fig. 19.1. *Eretes sticticus* prosternal process. Scale = 1.0mm.

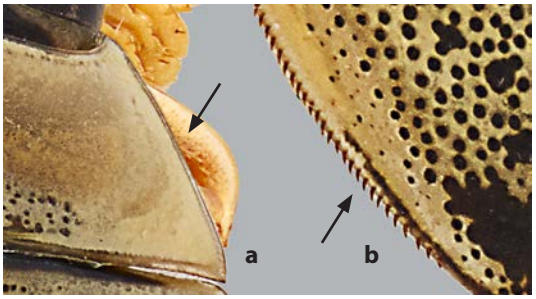


Fig. 19.2. *Eretes griseus*. **a**, Right lateral pronotal margin. **b**, Apicolateral margin of elytron.

Classification. This tribe is closely related to Aciliini based on both adult and larval features (Miller, 2000; 2001c; 2003; Ribera *et al.*, 2002b; 2008; Alarie *et al.*, 2011a; Miller and Bergsten, 2014a). Bukontaite *et al.* (2014) recovered Eretini as a strongly supported sister group to Aciliini.

Diversity. *Eretes* is the only genus in this tribe.

Natural History. See below under *Eretes*.

Distribution. See below under *Eretes*.

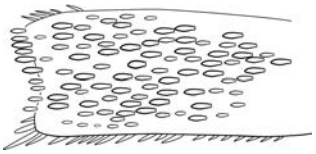


Fig. 19.3. *Eretes griseus* metatarsomere I, anterior surface.

Fig. 19.4. *Eretes griseus*. Scale = 1.0mm.

Genus *Eretes* Laporte, 1833

Diagnosis. This is the only genus in the tribe and is characterized by its diagnostic features (see above).

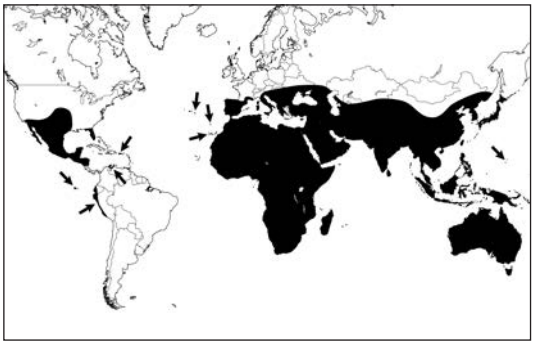
Classification. *Eretes* has been recognized in its own tribe for many years, and the species in the group are relatively homogeneous, though they are quite distinctive from other Dytiscidae.

Diversity. Four species are recognized, though there has been some contemporary disagreement about species limits (Larson *et al.*, 2000; Miller, 2002a). The group was revised by Miller (2002a).

Natural History. Members of *Eretes* are characteristic of shallow, temporary waters in arid regions, where they often occur in great numbers. They are extremely vagile and have dispersed to many island habitats and may be found in extremely isolated water bodies. They readily come to lights. They are well adapted to temporary aquatic habitats, where they can complete their larval stages in only 9–10 days (Kingsley, 1985). They have also been observed in synchronous emergence (Kingsley, 1985). Larvae were described by several investigators (Mayet,

1887; Meinert, 1901; Bertrand, 1948; Larson *et al.*, 2000; Miller, 2002a).

Distribution. This is a widespread group that is nearly circumtropical with species from Australia (including Tasmania), north through southern Asia to Indonesia and Japan and from numerous oceanic islands, throughout India and the Middle East, throughout Africa including Madagascar and several Atlantic islands, in southern Europe and in the New World from Peru and Venezuela north through the Caribbean to Florida and through Mexico to the southeastern and central United States (Map 19.1). This is the only dytiscid group with a species, *E. sticticus* (Linnaeus), that is distributed in both Africa and the New World (Miller, 2002a). Two species, *E. sticticus* and *E. griseus* (Fabricius), are together widespread in Africa (Miller, 2002a).



Map 19.1. Distribution of *Eretes*.

20. Tribe Aciliini

Body Length. 7.5–18.2mm.

Diagnosis. This tribe is easily diagnosed in the subfamily since both metatibial spurs are apically bifid (Fig. 20.1, convergent with *Laccophilus* in the Laccophilinae). Also, the line of bifid setae on the posterior surface of the metatibia is distinctly oblique with respect to the long axis of the tibia (Fig. 20.1), a synapomorphy with Eretini. Additionally, the meso- and metatarsomeres have series of golden setae along the apical margins (Fig. 20.2), a synapomorphy together with Eretini, Hydaticini, and Aubehydrini. Aciliines are medium to large, broadly oval beetles often with distinctive color patterns, maculae, and fasciae.

Classification. The tribe is well resolved in a clade with Eretini, Hydaticini, and Aubehydrini based especially on the presence of series of short, golden setae at the apical margins of meso- and metatarsomeres I–IV (Fig. 20.2) and DNA sequence data (Miller, 2001c; 2003; Miller and Bergsten, 2014a). Some analyses have suggested that either *Eretes* or *Notaticus* is nested within Aciliini (Ribera *et al.*, 2002b; 2008), but the current best evidence indicates that Eretini (*Eretes*) is sister to Aciliini (Bukontaite *et al.*, 2014) and Aubehydrini (*Notaticus*) is sister to that clade (Miller and Bergsten, 2014a).

Diversity. There are currently seven genera assigned to Aciliini.

Natural History. Most members of this group are found in ponds and marshes and other lentic habitats, including temporary pools. Some taxa are found in cool- or cold-water habitats. They are more rarely found in lotic habitats, but can be abundant in the margins of beaver ponds.

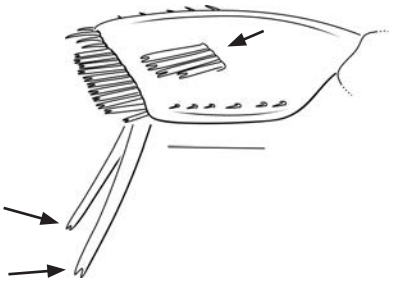


Fig. 20.1. *Acilius abbreviatus* left metatibia, posterior aspect. Scale = 1.0mm.

Distribution. Aciliines are found throughout the world with distinct faunas, and often endemic genera, in most biogeographic regions (Bukontaite *et al.*, 2014) except Australia, where aciliines are represented by only a single, relatively uncommon species of *Sandracottus* and the extremely widespread *Rhantaticus congestus* (Klug).

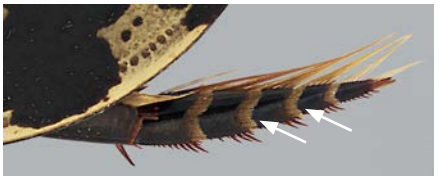


Fig. 20.2. *Sandracottus dejeani* left metatarsus.

Key to the Genera of Aciliini

1 Metacoxal lines absent or only indistinct (Fig. 20.3a) 2

1' Metacoxal lines distinct (Fig. 20.3b) 3

2(1) Mesofemur with longer ventral setae, at least some as long as ½ × width of mesofemur (Fig. 20.4a); body length greater (11.0–15.5mm); Oriental and Australian (Map 20.5) . . . . . *Sandracottus*, 130

2' Mesofemur with shorter ventral setae, less than ¼ × width of mesofemur (Fig. 20.4b); body length shorter (7.5–11.0mm); Afrotropical through southern Asia, and throughout the Oriental and Australian regions (Map 20.4) . . . . . *Rhantaticus*, 130

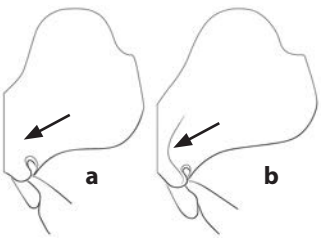


Fig. 20.3. Aciliini, left metacoxa. **a**, *Rhantaticus congestus*. **b**, *Graphoderus occidentalis*.

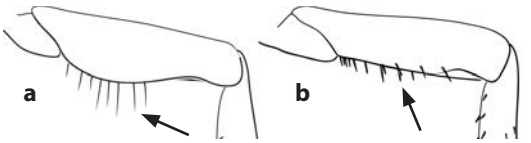


Fig. 20.4. Aciliini, mesoleg. **a**, *Sandracottus mixtus*. **b**, *Rhantaticus congestus*.

3(1) Surfaces of pronotum, elytron, metaventrite, metacoxae, and abdominal sterna with dense macropunctation (Fig. 20.5); females of many species with each elytron with four longitudinal sulci bearing short, suberect setae (Fig. 20.11b); Holarctic (Map 20.1) . . . *Acilius*, 127

3' Surfaces of pronotum, elytron, and ventral sterna with fine, sparse punctation; females without sulci 4

4(3) Anterior surface of metatibia without punctures or spines (Fig. 20.6a); Elongate "*Eretes*-like" body (Fig. 20.17); southeastern Africa (Map 20.7) . . . . . *Tikoloshanes*, 132

4' Anterior surface of metatibia with at least a few punctures or spines (Fig. 20.6b) 5

5(4) Abdominal sternum VI of male apically distinctly emarginate (Fig. 20.7a); male mesotarsomeres I–III with two rows of ventral adhesive setae (Fig. 20.8a); Afrotropical (Map 20.2) . . . . . *Aethionectes*, 128

5' Abdominal sternum VI of male apically evenly curved (Fig. 20.7b); male mesotarsomeres I–III with or without (Fig. 20.8b) ventral adhesive setae; Holarctic or Neotropical 6

6(5) Mesofemur with long ventral setae, some as long as 1 × width of mesofemur (Fig. 20.9a); mesotarsomeres I–III apically each with two long, stout setae as long as the tarsomeres (Fig. 20.9a); males without series of adhesive setae on mesotarsomeres I–III (Fig. 20.8b); females with bases of elytra covered with a field of short, aciculate striae (Fig. 20.10, the rare *T. zimmermani* with striae absent); Nearctic and Neotropical (Map 20.6) . . . *Thermonectus*, 131

6' Mesofemur with shorter ventral setae, about ½ × width of mesofemur (Fig. 20.9b); mesotarsomeres I–III with setae shorter than tarsomeres (Fig. 20.9b); males with or without series of adhesive setae on mesotarsomeres I–III; females without short, aciculate striae on elytra but may be granulate (Fig. 20.13c); Holarctic (Map 20.3) . . . . . *Graphoderus*, 128

Fig. 20.10. *Thermonectus nigrofasciatus* female.

Fig. 20.5. *Acilius sulcatus* elytra surface sculpture.

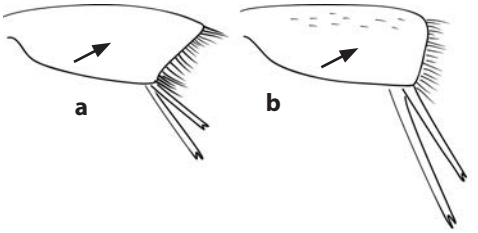


Fig. 20.6. Aciliini, right metatibia, anterior aspect. **a**, *Tikoloshanes eretiformis*. **b**, *Thermonectus margineguttatus*.

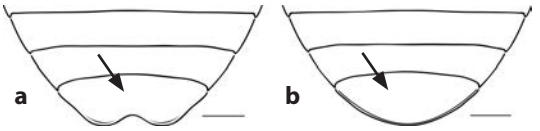


Fig. 20.7. Aciliini, last abdominal sternites. **a**, *Aethionectes fulvonotatus*. **b**, *Thermonectus nigrofasciatus*. Scales = 1.0mm.

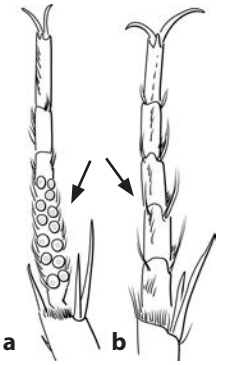


Fig. 20.8. Aciliini, mesotarsi, ventral aspect. **a**, *Aethionectes fulvonotatus*. **b**, *Thermonectus marmoratus*.

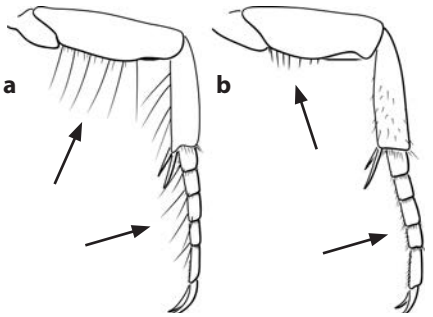


Fig. 20.9. Aciliini, mesoleg. **a**, *Thermonectus nigrofasciatus*. **b**, *Graphoderus occidentalis*.

Genus *Acilius* Leach, 1817

Body Length. 10.1–18.2mm.

Diagnosis. This genus is easily separable from other genera in the tribe by the surfaces of the pronotum, elytron, metaventrite, metacoxae, and abdominal sterna covered with large, dense punctures (Fig. 20.5). Females of most species (not all) also have four prominent longitudinal sulci on each elytron, which are thickly beset with short setae (Fig. 20.11b). These are large diving beetles, often with patterns of irrorations and black markings, which may be species specific (Fig. 20.11).

Classification. A comprehensive history of *Acilius* classification can be found in Bergsten and Miller (2006). The current classification and taxon content of *Acilius* — as a genus separate from *Hydaticus*, *Graphoderus,* and *Thermonectus* — dates largely to Schaum and von Kiesenwetter (1868) and Crotch (1873). *Acilius* was strongly supported as the sister group of the other Holarctic aciliine genus *Graphoderus* by Bukontaite *et al.* (2014), and the internal phylogeny of *Acilius* species was reconstructed by Bergsten and Miller (2007).

Diversity. Currently 13 species are recognized in the genus (Bergsten and Miller, 2006). *Acilius* was revised by Bergsten and Miller (2006), and species can be identified with keys therein.

Natural History. Members of this group are typically found in lentic situations, often with considerable vegetation, though sometimes in pools with a mud or peat substrate and in leaf-choked forest pools. Some species are relatively rare. One Japanese species (Yamazaki and Otsuki, 1993) and one Mediterranean species (Bergsten and Miller, 2006) are considered endangered. Several species are conspicuous and common in Europe and North America, and their biology has been studied somewhat more intensely, including their ecology (Arts *et al.*, 1981; Emets, 1983a–c; Yemetz, 1983; Abjornsson *et al.*, 1997; Davy-Bowker, 2002), physiology (Schmitz and Komnick, 1976), sperm morphology (Werner, 1976b), development and life history (Gewecke and Rostock, 1986; Okuno *et al.*, 1993; 1996; Yamazaki and Otsuki, 1993; Nakajima, 1995), behavior (Muggleton, 1966; Gewecke and Rostock, 1986), and chemistry (Chapman *et al.*, 1977; Newhart and Mumma, 1979). Larvae have been described by Fiori (1949), Wolfe (1980), Dettner (1982), Matta and Peterson (1987), Galewski (1991), and Nakajima (1995). Members of the group have dramatically modified male protarsi with protarsomeres 1–3 broadly expanded and bearing three large and a field of smaller adhesive discs. Some species also have a fringe of recurved setae around the disc. In addition, females of most species have each elytron with four broad, longitudinal grooves bearing suberect setae. These female modifications, which are common in the European species, were not overlooked by Darwin (1859), who suggested they acted as "aids" to the male during mating. Modern views on sexual antagonism theory suggest instead that they act as counter-weapons to male mating attempts, whereas the male protarsal modifications are grasping devices, giving them an advantage in the decision to mate (Bergsten and Miller, 2007). Modifications to the male protarsal suction discs and the female dorsal surface were shown to have coevolved by Berg-

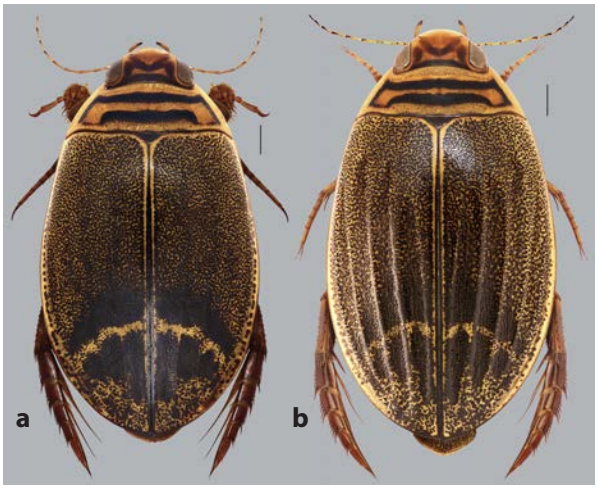


Fig. 20.11. *Acilius semisculatus*. **a**, Male. **b**, Female. Scales = 1.0mm.

sten and Miller (2005). Females of observed species behaviorally resist male mating attempts (Miller, 2003), which is consistent with this theory. Similar situations are thought to be operating in *Dytiscus*, *Hyderodes*, *Graphoderus*, *Thermonectus*, and possibly other Dytiscinae (Bergsten *et al.*, 2001; Miller, 2003; Bergsten and Miller, 2005; Miller and Bergsten, 2014b).

Distribution. *Acilius* is a Holarctic group with species distributed across the Nearctic Region south to Florida and Texas in the United States and in the Palearctic south to the northern coast of Africa, southern China, and Japan (Map 20.1). None of the species is shared between the Palearctic and Nearctic regions.

Map 20.1. Distribution of *Acilius*.

Genus *Aethionectes* Sharp, 1882

Body Length. 10.0–14.0mm.

Fig. 20.12. *Aethionectes apicalis*. Scale = 1.0mm.

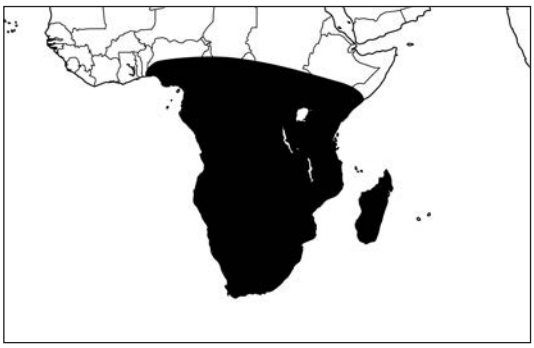
Diagnosis. Within Aciliini, this genus can be differentiated from all others by the following: (1) males with the apex of abdominal sternum VI distinctly emarginate (Fig. 20.7a); (2) males with two series of small, round adhesive setae ventrally on mesotarsomeres I–III (Fig. 20.8a); and (3) the anterior surface of the metatibia with at least some spines and punctures (as in Fig. 20.6b). The genus is very similar to *Tikoloshanes,* but that genus lacks punctures or setae on the anterior surface of the metatibia. These are medium to large species, often strikingly marked with distinct maculae or fasciae (Fig. 20.12).

Classification. *Aethionectes* was originally described to include a single African species (Sharp, 1882) with additional species added into the 1950s. The genus forms a sister-group relationship with *Tikoloshanes*, together forming an endemic Afrotropical clade (Bukontaite *et al.*, 2014).

Diversity. There are eight recognized species in the genus (Nilsson, 2001) that can be identified using the treatment by Guignot (1961).

Natural History. Specimens of many species are very rare in collections. Little is known of the biology of this group, but specimens have been collected from small forest pools with vegetation or dead leaves.

Distribution. *Aethionectes* are found in sub-Saharan Africa, including one species from Madagascar (Map 20.2). Given their relative rarity in collections, more survey work is needed to better establish the distributions of most species.



Map 20.2. Distribution of *Aethionectes*.

Genus *Graphoderus* Dejean, 1833

Body Length. 10.4–15.7mm.

Diagnosis. This genus is similar to *Thermonectus* in

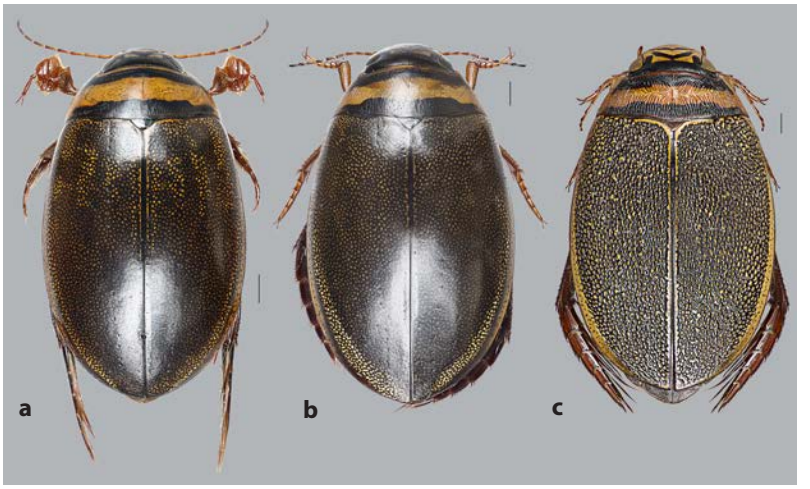


Fig. 20.13. *Graphoderus zonatus*. **a**, Male. **b**, Unmodified female. **c**, Modified female. Scales = 1.0mm.

many respects, except it has much shorter setae on the mesofemur, with their length less than half the width of the mesofemur (Fig. 20.9b), and the setae at the apex of mesotarsomeres I–III are relatively short (Fig. 20.9b). Males of all species except two have adhesive discs on mesotarsomeres I–III (as in Fig. 20.8a). Except for the species *G. liberus* (Say), the genus is very homogeneous with two transverse black markings across the pronotum (Fig. 20.13).

Classification. *Graphoderus* forms with *Acilius* a well-supported Holarctic clade (Bukontaite *et al.,* 2014). One Nearctic species, *G. liberus*, deviates significantly from the remaining species in the genus and a separate subgenus was suggested, but not described, by Larson *et al.* (2000).

Diversity. Diversity. There are 12 species and 1 subspecies in the genus after Holmgren *et al.* (2016) sorted out some confusion in the eastern Palearctic. Several are found across Europe and have been well known for a long time (e.g., Linnaeus, 1758). The Nearctic taxa have not been treated comprehensively, but Wallis (1939b) provided a thorough discussion of them, and they can be identified using Larson *et al*. (2000) or Holmgren *et al.* (2016). The Old World species can be identified using Holmgren *et al*. (2016) who also illustrated the male genitalia of all *Graphoderus* species.

Natural History. These species are found mainly in ponds with dense vegetation. Because of several prominent species occurring in Europe, the ecology and biology of some members of the genus have been investigated more than other Dytiscidae. Studies include aspects of their ecology (Denton, 1995; Schulte-Hostedde and Alarie, 2006), sensory structures (Leung and Zacharuk, 1986; Schaeflein, 1986; Jensen and Zacharuk, 1991; 1992), and chemistry (Miller and Mumma, 1973; Schaaf *et al*., 2000). One species, *G. bilineatus* (De Geer), is considered rare and endangered (Foster, 1996). Sperm conjugation in *G. liberus* was investigated by Higginson and Henn (2012). Larvae have been described by Galewski (1974a; 1975; 1990c). Two species, *G. zonatus* (Hoppe) and *G. elatus* Sharp, has populations with some females strikingly modified with dense rugose sculpturing on the pronotum and elytron (Fig. 20.13c) (Holmgren *et al.*, 2016). Bergsten *et al*. (2001) showed that in *G. zonatus* the frequency of these modified females in a population is correlated with the numbers and relative sizes of adhesive discs on the male protarsi, concluding that the correlation is related to a sexual antagonism scenario. Iversen *et al.* (2013) used *G. bilineatus* as a model for understanding large distributions of relatively rare species.

Distribution. *Graphoderus* is Holarctic with boreal representatives as far south as Florida in North America and south to Italy in Europe (Map 20.3). Eastern limits for some Palearctic species are poorly known, but the genus extends eastward to Japan.

Map 20.3. Distribution of *Graphoderus*.

Nilsson *et al*. (1999) suggested that the Nearctic species *G. perplexus* Sharp also occurs in the Palearctic, but this was revised by Holmgren *et al*. (2016) so that no species are now considered to be shared between the Nearctic and Palearctic, though this is currently being revised (Holmgren *et al*., in prep.).

Genus *Rhantaticus* Sharp, 1880

Body Length. 7.5–11.0mm.

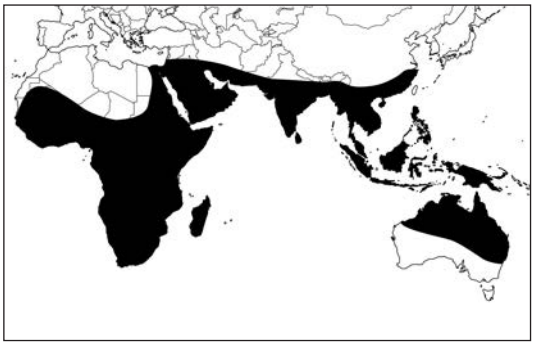
Diagnosis. This group differs from other aciliines except *Sandracottus* in having the metacoxal lines absent (Fig. 20.3a). From *Sandracottus* the genus differs in the relative length of the ventral setae on the mesofemur. In *Sandracottus* these setae are longer than half the width of the mesofemur (Fig. 20.4a), whereas in *Rhantaticus* they are less than one-fourth the width (Fig. 20.4b). These beetles are relatively small, elongate oval, and attractively and variably marked dorsally (Fig. 20.14).

Classification. This genus is most closely related to *Sandracottus*, which also has obscured metacoxal lines (Bukontaite *et al*., 2014).

Diversity. Currently, and historically, a single variable and widespread species, *R. congestus* Klug, is recognized (Guignot, 1961; Vazirani, 1968; Watts, 1978), but recent evidence indicates that multiple species are actually involved (Bergsten, unpublished, see Bukontaite *et al*., 2014).

Natural History. The species is found in a great many habitats, but especially temporary pools. Throughout its range it can often be exceptionally abundant and regularly comes to lights.

Distribution. *Rhantaticus congestus*, as currently defined, is among the most widespread species of Dytiscidae though this understanding may change as the taxon becomes better known. It occurs throughout Africa east through the Middle East and India to Southeast Asia, including the Philippines, and south to northern Australia and New Caledonia (Map 20.4).



Map 20.4. Distribution of *Rhantaticus*.

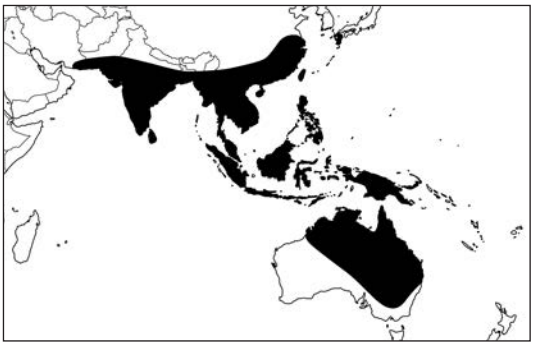
Genus *Sandracottus* Sharp, 1882

Body Length. 11.0–15.5mm.

Diagnosis. This group differs from other aciliines except *Rhantaticus* in having the metacoxal lines absent. From *Rhantaticus* the genus differs in the relative length of the ventral setae on the mesofemur. *Sandracottus* has setae that are longer than half

Fig. 20.14. *Rhantaticus congestus*. Scale = 1.0mm.

Fig. 20.15. *Sandracottus dejeani*. Scale = 1.0mm.



Map 20.5. Distribution of *Sandracottus*.

the width of the mesofemur (Fig. 20.4a), whereas in *Rhantaticus* they are less than 1/4 the width (Fig. 20.4b). These are moderately large beetles and are often very attractively marked dorsally with complex maculations or fasciae (Fig. 20.15).

Classification. This genus is sister clade to *Rhantaticus* (Bukontaite *et al.*, 2014).

Diversity. There are currently 16 species in the genus (Nilsson, 2001). *Sandracottus* has not been recently revised, and species can be identified using primarily Régimbart (1899) and certain regional faunas (e.g., Vazirani, 1968; Watts, 1978). The genus is currently under revision (L. Hendrich, in prep.).

Natural History. Specimens are found mainly in slow streams and ponds with emergent vegetation. Ninge Gowda and Vijayan (1992) investigated the effects of *S. festivus* (Illiger) on mosquito populations.

Distribution. *Sandracottus* species are found from India and Nepal throughout Southeast Asia, including south China and Japan, south through Australia (Map 20.5).

Genus *Thermonectus* Dejean, 1833

Body Length. 8.1–15.0mm.

Diagnosis. Within Aciliini, this group is characterized by having long ventral setae on the profemur (longer than the width of the profemur, Fig. 20.9a) and the female elytral surface, especially medially and basally, with a field of short, aciculate setae (Fig. 20.10, absent in one species, *T. zimmermani* Goodhue-McWilliams). Some of these species are among the most colorful dytiscids with some species black with bright yellow maculae or complex patterns of maculae and irrorations (Fig. 20.16).

Classification. This group was separated from *Acilius*, *Graphoderus*, *Hydaticus,* and related taxa early and has a long history of recognition in roughly its current composition. It is the sister group to all other aciliine genera, and the division between this mainly Neotropical group and the other aciliines with an Afrotropical origin was dated by Bukontaite *et al.* (2014) to a likely vicariance event.

Diversity. There are currently 19 species and 2 subspecies in the genus (Nilsson, 2001). The entire genus has been revised by Braga (2014).

Natural History. Members of *Thermonectus* are often among the most common medium-sized diving beetle species in lentic habitats in the New World. They are typical of marshes, ditches, roadside pools, forest pools, cattle ponds, etc. A couple southwestern North America species are dramatically colored with yellow maculae on black backgrounds. These species are typical of desert rock pools, where they are

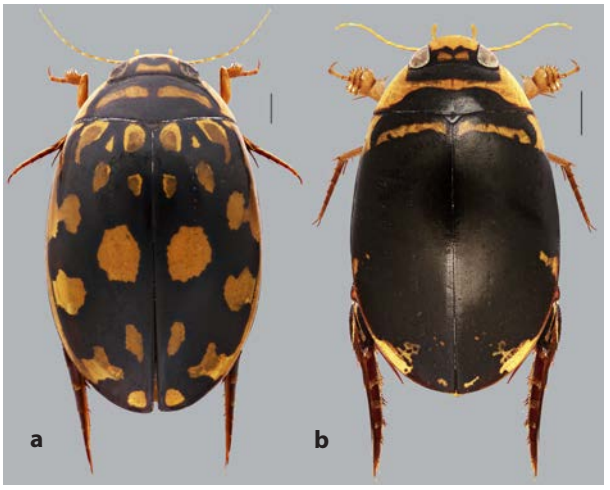


Fig. 20.16. *Thermonectus* species. **a**, *T. marmoratus*. **b**, *T. nobilis*. Scales = 1.0mm.

often conspicuous and possibly aposematic (Young, 1960; Larson, 1996a). Larvae have been described by Carroll and Barman (2004) and Michat and Torres (2005b). Steroids have been characterized from the prothoracic defensive glands in *T. marmoratus* (Gray) (Meinwald *et al.*, 1998). *Thermonectus marmoratus* has become popular in insect zoos (Morgan, 1992). Other aspects of their biology have been investigated, including toxicity of riceland agricultural chemicals on *T. basillaris* (Harris) (Apgar *et al.*, 1985) and feeding habits in *T. marmoratus* (Velasco and Millan, 1998). *Thermonectus marmoratus* larval eyes and vision have been the subject of considerable recent investigation (Mandapaka *et al.*, 2006; Maksimovic *et al.*, 2009; 2011; Stecher *et al.*, 2010; Stowasser and Buschbeck, 2012; 2014; Bland *et al.*, 2014).

Distribution. This is a New World group with species occurring from Canada throughout much of North America and south throughout Central and South America (Map 20.6).

Map 20.6. Distribution of *Thermonectus*.

Genus *Tikoloshanes* Omer-Cooper, 1956

Body Length. 13.5–15.5mm.

Diagnosis. The single species in this genus is distinguishable from all other genera in the tribe by the following: (1) males with the apex of abdominal sternum VI distinctly emarginate (as in Fig. 20.7a); (2) males with two series of small, round adhesive setae ventrally on mesotarsomeres I–III (as in Fig. 20.8a); and (3) anterior surface of the metatibia without spines and punctures (Fig. 20.6a). The genus is very similar to *Aethionectes*, but that genus has at least a few punctures or setae on the anterior surface of the metatibia (as in Fig. 20.6b). Superficially *T. eretiformis* Omer-Cooper looks much like members of *Eretes* (see Fig. 19.4) but lacks the numerous apomorphies present in that group.

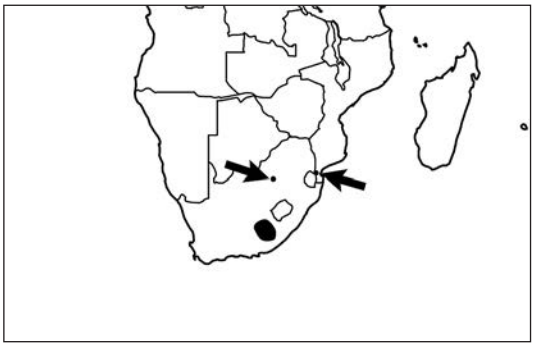
Fig. 20.17. *Tikoloshanes eretiformis*. Scale = 1.0mm.

Classification. The phylogenetic position of *Tikoloshanes* was tested by Bukontaite *et al.* (2014) and it was inferred to be sister to *Aethionectes*. These genera share the distinct apical emargination on the male abdominal sternum VI (Omer-Cooper, 1965b).

Diversity. There is only a single, poorly known species in the genus, *T. eretiformis*.

Natural History. This is a very rarely collected beetle and nothing is known of the biology. One specimen was collected from a farmland pond with emergent vegetation at an altitude of 1,400m.

Distribution. The single species is known only from South Africa and southern Mozambique (Map 20.7).



Map 20.7. Distribution of *Tikoloshanes*.

21. Subfamily Coptotominae

Body Length. 5.7–8.6mm.

Diagnosis. Although superficially distinctive, this subfamily is difficult to characterize and relatively generalized within the family. They are similar to matines, lancetines, copelatines, and colymbetines. The primary diagnostic character combination is: (1) the pronotum has a well-developed lateral bead (Fig. 21.1); (2) the metacoxal lobes are large and rounded with the metacoxal lines not closely approximated (Fig. 21.2a); (3) the prosternum and prosternal process are in the same plane though the anterior margin ascends significantly to the base of the head (Fig. 21.2b); (4) the pro- and mesotarsi are distinctly pentamerous (Fig. 21.2d); (5) the scutellum is visible (Fig. 21.3); (6) metatarsomeres I–IV have the ventral apical angles lobed (Fig. 21.2a); (7) the apical palpomere of both the maxillary and labial palps are distinctly bifid (Fig. 21.2c); and (8) the metatarsal claws are subequal in length in both sexes (Fig. 21.2e). Many of these features are evidently retained plesiomorphies. Also, specimens are medium sized, elongate, and relatively narrow and streamlined, and most species have the elytra variously irrorate and patterned with light and dark regions (Fig. 21.3).

Classification. This group was one of several "unassociated" groups of "Colymbetides," according to Sharp (1882). Historically, this family group has been recognized mainly at tribe rank within Colymbetinae, and less commonly as its own subfamily

Fig. 21.1. *Coptotomus longulus*. Right pronotal margin.

(e.g., Bacon *et al.,* 2000). Miller (2001c) placed it at subfamily rank, and this is supported by recent phylogenetic analyses (Ribera *et al.,* 2002b; 2008; Miller and Bergsten, 2014a), though the group has an enigmatic relationship with other diving beetles. Ribera *et al.* (2008) found it closely associated with Copelatinae, but Miller and Bergsten (2014a) found it sister to Hydrodytinae + Hydroporinae, though with modest support.

Diversity. *Coptotomus* is the only genus in the subfamily.

Natural History. See below under *Coptotomus*.

Distribution. See below under *Coptotomus*.

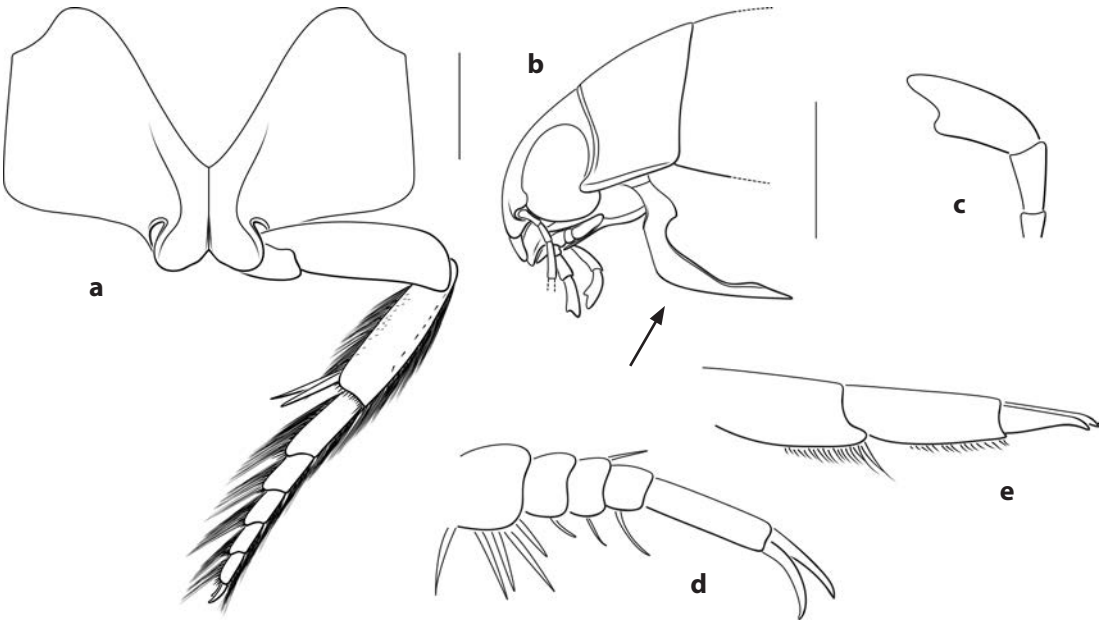


Fig. 21.2. *Coptotomus longulus* features. **a**, Metacoxae and left metaleg. **b**, Lateral aspect. **c**, Labial palp. **d**, Protarsomeres. **e**, Metatarsomeres and claws. Scales = 1.0mm.

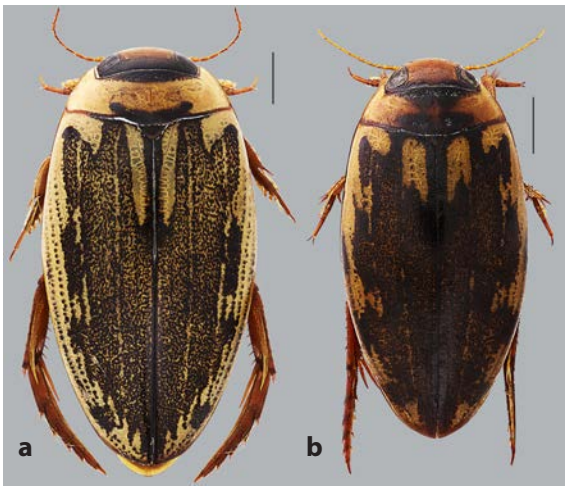


Fig. 21.3. *Coptotomus* species. **a**, *C. longulus*. **b**, *C. interrogatus*. Scales = 1.0mm.

Genus *Coptotomus* Say, 1830

Diagnosis. This is the only genus in the subfamily and is characterized by its diagnostic combination (see above). Specimens are elongate and relatively slender with extensive dorsal irregular irroration (Fig. 21.3).

Classification. See above for discussion of classification of the single genus, *Coptotomus*.

Diversity. There are five species and one subspecies currently recognized in *Coptotomus* following Larson *et al.* (2000). The eastern North American species were revised by Hilsenhoff (1980), but the western North American diversity has not been adequately revised, and there may be multiple species involved (Hilsenhoff, 1980).

Natural History. Specimens are often collected in permanent ponds or slow streams with much vegetation. Larvae have been described for some species (Wilson, 1923; Barman, 1972; Bacon *et al.,* 2000). Larvae of *Coptotomus* are the only diving beetles with external gills along the sides of the abdomen (see Fig. 2.5k, Michat and Alarie, 2013). Some additional aspects of *Coptotomus* biology were presented by Bacon *et al.* (2000). Among other things, they note that larvae of *C. longulus lenticus* Hilsenhoff are benthic inhabitants of ponds.

Distribution. This Nearctic taxon occurs across much of Canada and the United States south through much of northern and central Mexico (Map 21.1).

Map 21.1. Distribution of *Coptotomus*.

22. Subfamily Hydrodytinae

Body Length. 2.1–3.8mm.

Diagnosis. Within Dytiscidae this subfamily can be diagnosed by the following character combination: (1) the scutellum is visible with the elytra closed (Figs. 22.5,6); (2) the pro- and mesotarsi are distinctly pentamerous in both sexes (Fig. 22.1); (3) the prosternum and prosternal process are in the same plane and do not have a median prominence or tubercle; and (4) the gonocoxae have a prolonged anterior apodeme (Fig. 22.4). The rami of the female genitalia are sinuate in all known species (Fig. 22.4), and the male median lobe is bilaterally asymmetrical in the single species with known males (Fig. 22.2).

Classification. Hydrodytinae is generalized within Dytiscidae. The female gonocoxa has a distinct, long anterior apodeme (Fig. 22.4), which makes them similar to Hydroporinae, but the scutellum is visible with the elytra closed (Figs. 22.5,6) and the male median lobe is bilaterally asymmetrical in the male specimens known (Fig. 22.2), unlike many Hydroporinae, which have the median lobe bilaterally symmetrical, at least as a plesiomorphy (Miller, 2001c). The metafurca is also similar to hydroporines (Miller, 2001c). Members of this group were historically placed in the copelatine genus *Agaporomorphus*, but that genus was subdivided by Miller (2001c), who erected a new genus and subfamily to include certain unusual species based in large part on features of the female genitalia. The group was resolved as sister to all Hydroporinae in the phylogeny developed by Miller (2001c) but was resolved as sister to Matinae in the analysis by Ribera *et al.* (2008). A larger combined analysis by Miller and Bergsten (2014a) resulted in, again, a sister-group relationship between Hydrodytinae and Hydroporinae with good support. The entire subfamily was revised by Miller (2002b), including description of a new genus, *Microhydrodytes* Miller.

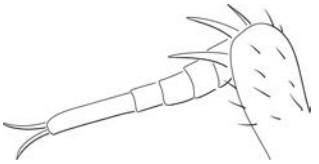


Fig. 22.1. *Hydrodytes inaciculatus*, left protarsus and protibia.

Diversity. The subfamily includes two genera, *Hydrodytes* and *Microhydrodytes*.

Natural History. Most of the specimens in museums were collected at lights. A few specimens (of *Hydrodytes*) have been collected from pools of water in tropical forest and sandy forest streams with dense leaf pack. In general, the group is very rarely collected, and very little is known of its natural history.

Distribution. This is a lowland tropical group from southern Brazil north to Trinidad and Honduras. One species of *Hydrodytes* has been collected once in Florida, USA (Young, 1989a).

Fig. 22.2. *Hydrodytes inaciculatus*, male genitalia, median lobe, right lateral aspect, median lobe, ventral aspect, right lateral lobe, right lateral aspect.

Key to the Genera of Hydrodytinae

1 Dorsal surface usually with opalescent sheen; without punctation or with punctures small and indistinct (Fig. 22.5); larger (>2.5mm); antennomeres long and slender (Fig. 22.3a) . . . . . *Hydrodytes*, 136

1' Dorsal surface without opalescent sheen; with small but distinct punctures on elytra (Fig. 22.6); small (<2.2mm); antennomeres short and broad (Fig. 22.3b) . . . . . *Microhydrodytes*, 136

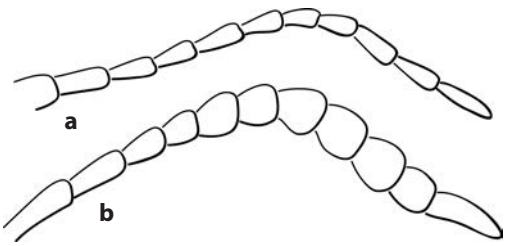


Fig. 22.3. Right antenna. **a**, *Hydrodytes opalinus*. **b**, *Microhydrodytes elachistus*.

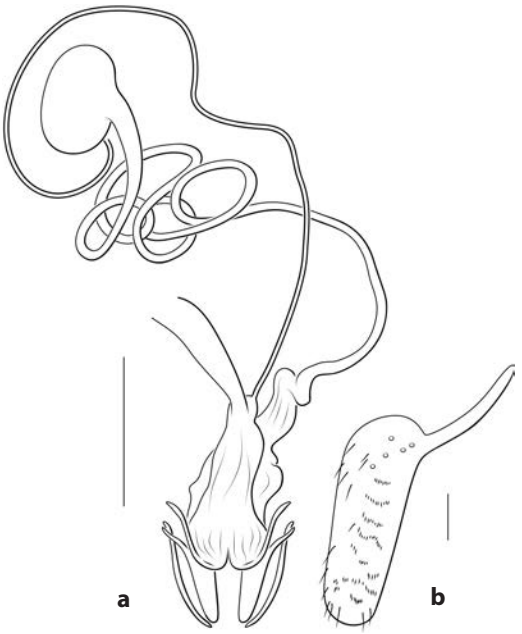


Fig. 22.4. *Hydrodytes inaciculatus*. **a**, Female reproductive tract, ventral aspect. **b**, Gonocoxa. Scales = 0.5mm (a) 0.1mm (b).

Genus *Hydrodytes* Miller, 2001

Body Length. 2.6–3.8mm.

Diagnosis. *Hydrodytes* differ from *Microhydrodytes* in having the dorsal surface with an iridescent (opalescent) sheen and lacking significant punctation on the elytra (Fig. 22.5). The antennomeres are relatively longer (Fig. 22.3a). Although small, members of the genus are larger than *Microhydrodytes*.

Classification. All known species of *Hydrodytes* were originally described in the Copelatinae genus *Agaporomorphus*. Miller (2001c) divided that genus and erected *Hydrodytes* (and the subfamily), recognizing similarities with hydroporines in the female reproductive tract. Phylogeny of the genus was investigated by Miller (2002b).

Fig. 22.5. *Hydrodytes opalinus*. Scale = 1.0mm.

Diversity. Three species are recognized in the genus, but lack of male specimens and few known female characters have made species delimitations problematic. There may be additional species involved. The genus was revised by Miller (2002b) and discussed by Young (1989a) and Zimmermann (1921) (the latter two as *Agaporomorphus*).

Natural History. Little is known of the natural history of this apparently rare (at least rarely collected) genus. Most museum specimens were collected at lights in tropical forests. A few specimens have been collected in forest pools and streams, but only rarely. The apparent absence of males in two of the three species is curious and suggestive, at least, of the possibility of parthenogenesis in these species, a condition in Dytiscidae that has been reported also in the genus *Belladessus* (Bidessini) (Miller and Short, 2015). However, no dispositive evidence for parthenogenetic reproduction has yet been presented for these beetles. All three species appear to have normal female reproductive tracts (Fig. 22.4).

Distribution. The genus is known mainly from lowland South and Central America with one species from southern Florida, USA (Map 22.1).

Map 22.1. Distribution of *Hydrodytes*.

Genus *Microhydrodytes* Miller, 2002

Body Length. 2.1mm.

Fig. 22.6. *Microhydrodytes elachistus*, holotype. Scale = 1.0mm.

Diagnosis. This genus differs from *Hydrodytes* in having elytra without an opalescent sheen and with fine but distinctive punctation (Fig. 22.6). Also, the antennomeres are short and broad (Fig. 22.3b), and the overall body size is very small.

Classification. The placement of *Microhydrodytes* in Hydrodytinae is based mainly on female genitalic characters and presence of a visible scutellum with the elytra closed (Miller, 2002b). The single species is unusual, and its relationship with *Hydrodytes* is not completely certain.

Diversity. Only a single female specimen of a single species, *M. elachistus* Miller, is known in this genus. The genus was treated by Miller (2002b).

Natural History. The single known specimen was collected at a black light trap (Miller, 2002b).

Distribution. *Microhydrodytes* are known only from Parque Nacional Xingu, Mato Grosso, Brazil (Map 22.2).

Map 22.2. Distribution of *Microhydrodytes.*

23. Subfamily Hydroporinae

Body Length. 0.9–7.8mm.

Diagnosis. Because of the size and diversity of this group, it is difficult to generalize about its morphology. However, there are a few characters that are diagnostic of hydroporines, though some are modified secondarily in many taxa. The main set of diagnostic characters are the following: (1) the anteromedial portion of the prosternum is in a distinctly different plane than the prosternal process (i.e., the prosternal process is declivous with respect to the prosternum) (Fig. 23.1), though this is less pronounced in certain taxa such as *Lioporeus* (Fig. 23.1b); (2) the pro- and mesotarsi are pseudotetramerous with tarsomere IV small and hidden within the lobes of tarsomere III (Fig. 23.2b), though some taxa, such as *Bidessonotus* (see Fig. 37.31a), *Necterosoma* (Fig. 23.2a) and *Sternopriscus*, have the pro- and mesotarsi more distinctly pentamerous, and males of *Tiporus*, *Antiporus,* and *Sekaliporus* have the tarsi truly tetra- or trimerous (see Fig. 30.8e,f); and (3) the scutellum is concealed with the elytra closed (Fig. 23.8b), though *Celina* and *Carabhydrus* have a clearly visible scutellum (Fig. 23.8a,c) and a few other taxa — e.g., *Hydrocolus* (see Fig. 27.10) — have the scutellum partially visible. Hydroporines are generally small (length usually < 5mm), and most of the small diving beetles in the family are in this group, though there is broad overlap in extreme size range between hydroporines and other subfamilies. In other respects, members of hydroporines are extremely diverse in body shape and other characters, and this

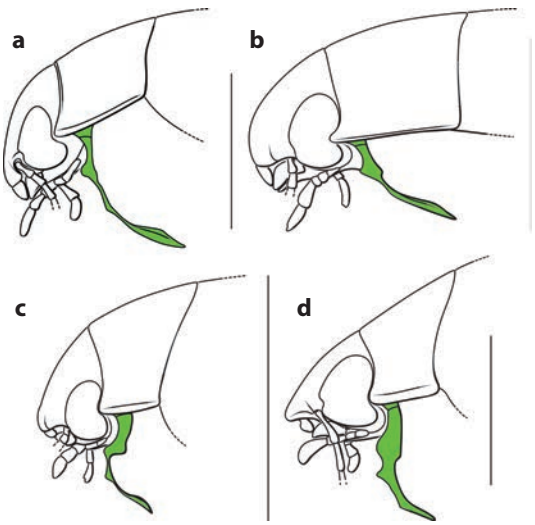


Fig. 23.1. Hydroporinae prosternal processes, lateral aspect. **a**, *Coelambus impressopunctatus*. **b**, *Lioporeus triangularis*. **c**, *Microdytes sabitae*. **d**, *Pachydrus princeps*. Scales = 1.0mm.

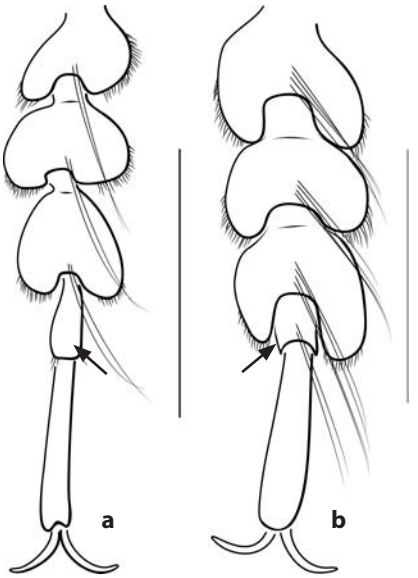


Fig. 23.2. Hydroporinae protarsi. **a**, *Necterosoma penicillatum*. **b**, *Barretthydrus tibialis*. Scales = 1.0mm.

is the most morphologically diverse group in nearly every character system within the Dytiscidae. This group includes the great majority of subterranean diving beetles, which are difficult to diagnose using typical characters used for epigean taxa.

Classification. The composition of this subfamily has not changed much, though two tribes currently included in Hydroporinae have been recognized at subfamily rank, Vatellini (Omer-Cooper, 1958b) and Methlini (Omer-Cooper, 1958b; Franciscolo, 1966; Bilardo and Rocchi, 1990; Trémouilles, 1995). There is little doubt that these two groups are nested well within Hydroporinae (Wolfe, 1985; 1988; Miller, 2001c; Ribera *et al.*, 2002b; 2008; Miller and Bergsten, 2014a). There have been relatively few comprehensive, concentrated phylogenetic analyses internally in Hydroporinae, though Wolfe (1985; 1988) made significant advances in developing an understanding of the tribes Laccornini, Methlini, and certain other taxa characterized by plesiomorphic states. Other large-scale analyses have clarified relationships among the tribes as well (Miller, 2001c; Ribera *et al.*, 2002b; 2008; Miller and Bergsten, 2014a). One terrestrial and several subterranean genera are currently *incertae sedis* for tribe.

Diversity. There are 10 tribes, 4 subtribes and 118 genera currently recognized in this dytiscid subfamily. There are more species in this group than any other diving beetle subfamily with over half the total species diversity of diving beetles (see Fig. 2.3).

There are also the greatest number of genera in the subfamily as well, and considerable use is made of the tribe rank to organize this diversity.

Natural History. As with all other aspects of this subfamily, the natural history and biology of this group is dramatically diverse. Species live in all habitats in which diving beetles are known, from lentic to lotic situations, springs, moss mats, hygropetric habitats, subterranean aquifers, hyporheic zones, and in terrestrial leaf litter. Often huge numbers of specimens and great diversity can be found in any given habitat.

Distribution. Species in this group occur throughout the world with distinct faunas in each region. They occur from extreme northern latitudes and include the most northerly occurring diving beetles to extremely remote habitats such as oceanic islands.

Key to the Tribes of Hydroporinae

Several genera in this group are subterranean with depigmentation, reduced eyes and flight ability, and other features associated with stygobitic lifestyles. Some of these are placed within existing tribes of Hydroporinae and others are currently classified as *incertae sedis* with respect to Hydroporinae tribes. These are keyed out separately in the key to subterranean taxa (page 45).

1 Metepiventrite not reaching mesocoxal cavities externally, separated by mesepimeron (Fig. 23.3a); prosternal process not reaching to metaventrite, mesocoxae contiguous (Fig. 23.4a) . . . . . Vatellini, 190

1′ Metepiventrite reaching mesocoxal cavities (Fig. 23.3b); prosternal process reaching metaventrite separating mesocoxae (Fig. 23.4b) except in several rare subterreanean and hyporheic taxa, South African *Andex*, and the North American *Stictotarsus minipi* 2

2(1) Metatarsal claws distinctly unequal in length, anterior shorter than posterior (Fig. 23.5a); metacoxal lobes absent (Fig. 23.6a,b) or extremely small (Fig. 23.6c) 3

2′ Metatarsal claws equal or subequal in length (Fig. 23.5b); metacoxal lobes present, generally larger (Fig. 23.6d,e), though small in some taxa (see Fig. 26.6e). 4

3(2) Prosternal process apically narrow, acute (Fig. 23.6a, bifid in males of some *Desmopachria*, see Fig. 36.18); metasternal wing narrow medially (Fig. 23.6a) . . . . . .Hyphydrini, 207

3′ Prosternal process apically broad, truncate, in broad contact with metaventrite (Fig. 23.6b); metasternal wing broad medially (Fig. 23.6b) . . . . . Pachydrini, 199

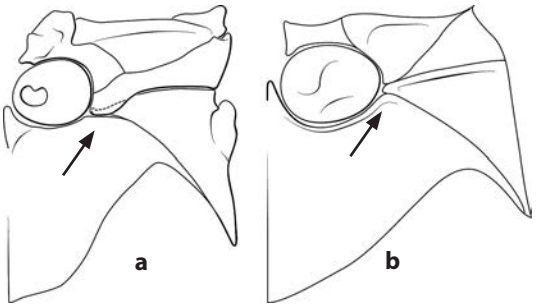


Fig. 23.3. Hydroporinae, left thoracic sternites. **a**, *Vatellus grandis*. **b**, *Hydroporus dichrous*.

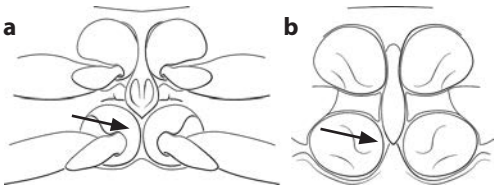


Fig. 23.4. Hydroporinae prosternum, prosternal process and pro- and mesocoxae. **a**, *Derovatellus lentus*. **b**, *Hydroporus dichrous*.

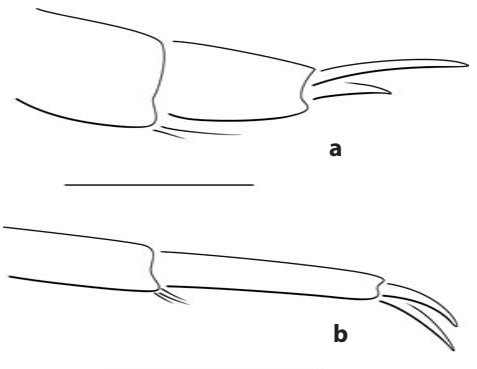


Fig. 23.5. Hydroporinae metatarsomeres IV–V and metatarsal claws. **a**, *Microdytes sabitae*. **b**, *Coelambus patruelis*. Scales = 0.1mm (a) and 0.25mm (b).

4(2) Prosternal process short and apically broadly truncate (Fig. 23.6d); metacoxal process apically broad, with prominent lateral lobes subtended by distinct medial emarginations (Fig. 23.6d); female gonocoxae either fused and knife-like with long laterally projecting anterior projections (see Fig. 33.3a) or not fused and each apically trilobed (Fig. 33.3b) . . . . . Hydrovatini, 196

4′ Prosternal process elongate and apically narrowly pointed or rounded (Fig. 23.6e); metacoxal process various, but not broad with prominent lobes subtended by distinct emarginations (in Methlini metacoxae moderately broad and with large, rounded metacoxal lobes with distinct sublateral emarginations (see Fig. 32.1a), but prosternal process apically narrow); female gonocoxae various, but not fused and knife-like with long anterolateral projections and not apically trilobed 5

5(4) Abdomen and elytron apically acuminate (Fig. 23.7); scutellum visible (*Celina*, Fig. 23.8a) or not (*Methles*, Fig. 23.8b) with elytra closed, pronotum not cordate (Fig. 23.8a,b) . . . . . Methlini, 194

5′ Abdomen and elytron apically rounded or pointed, but not acuminate; scutellum not visible or only partly (*Hydrocolus*, Fig. 27.10), or more visible but body elongate with pronotum cordate (*Carabhydrus*, Fig. 23.8c) 6

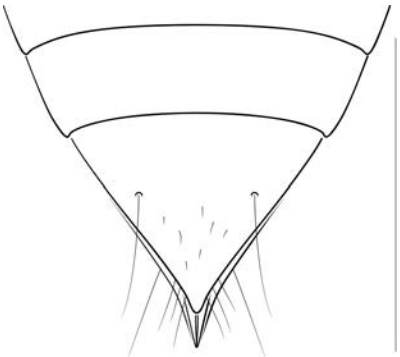


Fig. 23.7. *Methles cribratellus* abdominal apex, ventral aspect. Scale = 1.0mm.

6(5) Dorsal margin of metafemur extending to metacoxal lobe (Fig. 23.9a); metacoxal lobes large and rounded (Fig. 23.9a). 7

6' Dorsal margin of metafemur separated from metacoxal lobe by metatrochanter (Fig. 23.9b); metacoxal lobes usually smaller, modified, generally narrowly rounded or subtriangular (Fig. 23.9b) 8

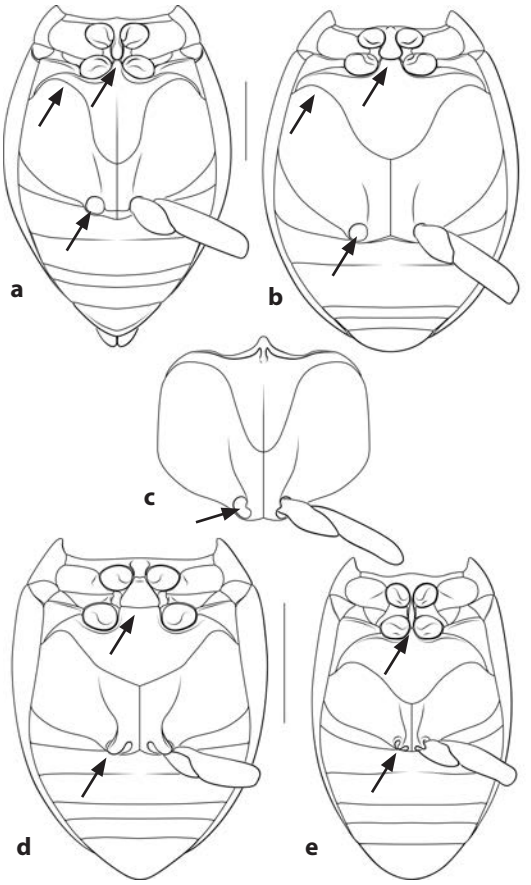


Fig. 23.6. Hydroporinae venters. **a**, *Hyphydrus* sp. **b**, *Pachydrus princeps*. **c**, *Anginopachria ullrichi*. **d**, *Hydrovatus cardoni*. **e**, *Coelambus patruelis*. Scales = 1.0mm.

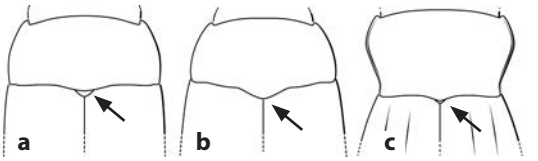


Fig. 23.8. Hydroporinae dorsal surfaces. **a**, *Celina hubbelli*. **b**, *Methles cribratellus*. **c**, *Carabhydrus niger*.

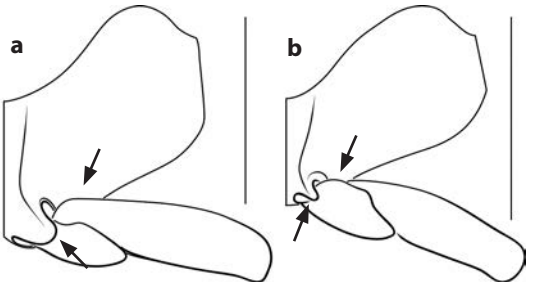


Fig. 23.9. Hydroporinae left metacoxa, metatrochanter, and metafemur. **a**, *Laccornis oblongus*. **b**, *Coelambus patruelis*. Scales = 1.0mm.

7(6) Laterotergite of female genitalia absent (Fig. 23.10a); southern Neotropical and Afrotropical . . . . . Laccornellini, 147
7′ Laterotergite of female genitalia present (Fig. 23.10b); Holarctic . . . . . Laccornini, 145

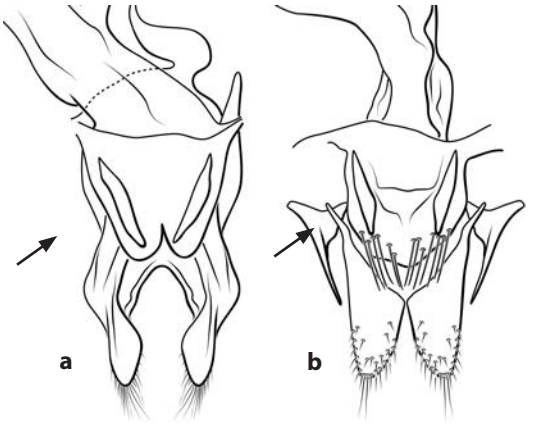


Fig. 23.10. Hydroporinae female reproductive tract, ventral aspect. **a**, *Laccornellus copelatoides*. **b**, *Laccornis oblongus*.

8(6) Metatibia elongate, apically gradually expanded in most taxa (Fig. 23.11a); metacoxal lobes very small, metacoxal process at same level as abdomen (Fig. 23.11a, except in *Peschetius*); male lateral lobe of most groups with two (Fig. 23.12a) or three (Fig. 23.12b) segments, some with only one (Fig. 23.12c) . . . Bidessini, 219
8′ Metatibia various but not gradually expanded (Fig. 23.11b); metacoxal lobes larger, conspicuous, posterior margin of metacoxal process distinctly separated from level of abdomen (Fig. 23.11b); male lateral lobe with one segment (Fig. 23.12d); 9

9(8) Elytral epipleuron with transverse carina at humeral angle (Fig. 23.13a). . . . . Hygrotini, 201
9′ Elytral epipleuron without transverse carina at humeral angle (Fig. 23.13b) . . . . . Hydroporini, 150

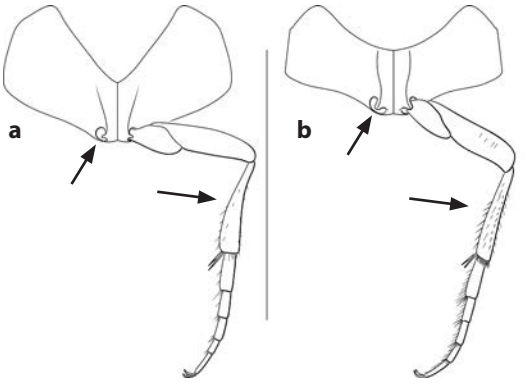


Fig. 23.11. Hydroporinae metacoxae and left metaleg. **a**, *Uvarus lacustris*. **b**, *Heterosternuta wickhami*. Scales = 0.5mm (a) and 1.0mm (b).

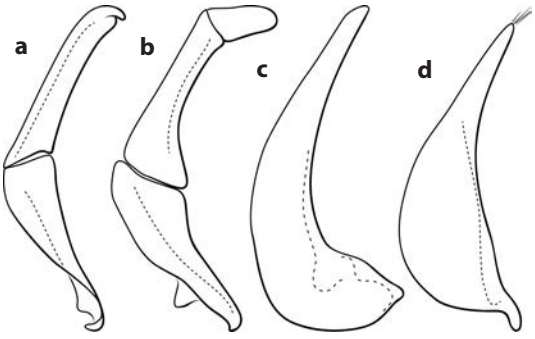


Fig. 23.12. Hydroporinae right lateral lobes. **a**, *Liodessus affinis*. **b**, *Hydroglyphus lineolatus*. **c**, *Hydrodessus surinamensis*. **d**, *Heterosternuta wickhami*.

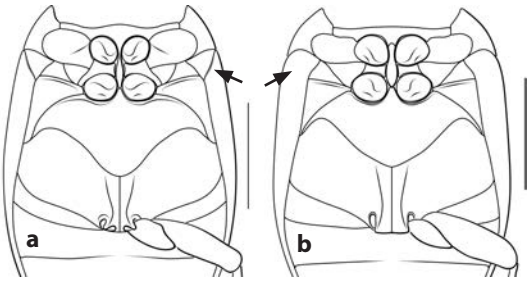


Fig. 23.13. Hydroporinae ventral surfaces. **a**, *Coelambus patruelis*. **b**, *Hydroporus dichrous*. Scales = 1.0mm.

Genus *Kuschelydrus* Ordish, 1976

Body Length. 1.5–1.6mm.

Diagnosis. *Kuschelydrus* are morphologically modified for a hyporheic lifestyle with reduced eyes, depigmentation, and flightlessness. The single species is similar to *Phreatodessus* but has the lateral margins of the body more parallel-sided and not so discontinuous between the pronotum and elytron (Fig. 23.14).

Classification. As with *Phreatodessus*, Ordish (1976a) placed this genus in Bidessini, but the male lateral lobes have only a single segment. Biström (1988b) did not include it in Bidessini, and it has remained *incerta sedis* in Hydroporinae since that time.

Diversity. There is a single species, *K. phreaticus* Ordish.

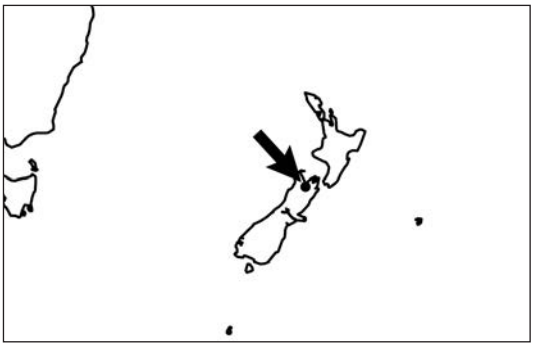
Natural History. Specimens of *Kuschelydrus* are hyporheic and have been collected from boreholes into alluvial deposits (Ordish, 1976a). A number of

Fig. 23.14. *Kuschelydrus phreaticus*. Scale = 1.0mm.

Fig. 23.15. *Morimotoa phreatica*. Scale = 1.0mm.

details about the biology of the species were documented by Ordish (1976a).

Distribution. *Kuschelydrus phreaticus* are found only in the Waimea River area near Nelson in New Zealand (Map 23.1).



Map 23.1. Distribution of *Kuschelydrus*.

Genus *Morimotoa* Uéno, 1957

Body Length. 2.5–4.1mm.

Diagnosis. *Morimotoa* are morphologically modified for a subterranean lifestyle with reduced eyes, depigmentation, and flightlessness. Although species are similar to each other, the group is difficult to diagnose. Among subterranean Hydroporinae they are quite generalized without eyes, striae on the pronotum or elytra, and other significant modifications (Fig. 23.15).

Classification. *Morimotoa* was among the first subterranean genera of diving beetles described and was originally placed in Hydroporini (Uéno, 1957), which was later supported by larval morphology (Bertrand, 1972) and in comparison with other described subterranean taxa (Young and Longley, 1976; Franciscolo, 1979b; 1983; Spangler, 1986). Ordish (1976a), however, put *Morimotoa* in Bidessini with his new *Kuschelydrus* and *Phreatodessus*, along with *Siettitia*, though they were later excluded from the tribe by Biström (1988b), a conclusion supported by Ordish (1991). Smrž (1983) put all the subterranean hydroporines in a single tribe, Siettitiini Smrž, though this group as he defined it is clearly polyphyletic (e.g., Bameul, 1989; Ribera and Faille, 2010). Nilsson *et al.* (1989) regarded several of these genera as *incerta sedis* with respect to tribe, though Uéno (1996) later expressed a preference for placement of *Morimotoa* (and the other subterranean genera known at that time) among Hydroporini.

Diversity. There are currently three species and one subspecies in the genus that were treated by Uéno (1957; 1996).

Natural History. These species are found in subterranean waters of Japan (accessed by wells), where they have been found also with species of the Noteridae genus *Phreatodytes* Uéno. Some of them

Map 23.2. Distribution of *Morimotoa*.

(such as *M. gigantea* Uéno) may have been adversely affected by human activities and may be extinct (Uéno, 1996).

Distribution. *Morimotoa* are found in central Japan (Map 23.2).

Fig. 23.16. *Phreatodessus hades*. Scale = 1.0mm.

Genus *Phreatodessus* Ordish, 1976

Body Length. 1.6–2.5mm.

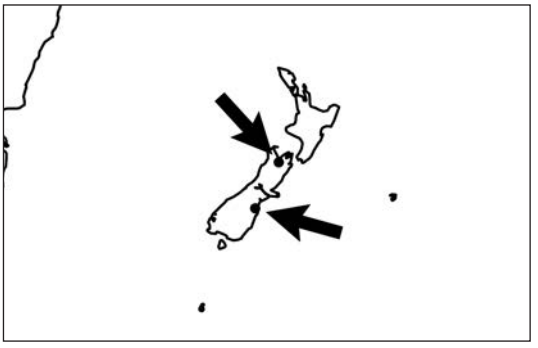
Diagnosis. The single species is morphologically modified for a hyporheic lifestyle with reduced eyes, depigmentation, and flightlessness. The species is similar to *Kuschelydrus,* but the lateral margins of the body are more more discontinuous between the pronotum and elytron (Fig. 23.16).

Classification. As with *Kuschelydrus*, Ordish (1976a) placed this genus in Bidessini, but the male lateral lobes are single-segmented. Biström (1988b) did not include it in the tribe, and it has remained *incerta sedis* in Hydroporinae since then.

Diversity. There are two species, *P. hades* Ordish and *P. pluto* Ordish.

Natural History. Specimens of *Phreatodessus* are hyporheic and have been collected from boreholes into alluvial deposits (Ordish, 1976a). General details of the biology of the species were documented by Ordish (1976a).

Distribution. *Phreatodessus* has been found in the Waimea River area near Nelson and in a borehole at Rua Pae Farm, Dalgety AgriResearch Station, Canterbury, New Zealand (Map 23.3).



Map 23.3. Distribution of *Phreatodessus*.

Genus *Typhlodessus* Brancucci, 1985

Body Length. 1.25mm.

Diagnosis. *Typhlodessus*, like other terrestrial diving beetles, lack swimming hairs. Unique features include the presence of five distinct costae on each elytron (Fig. 23.17), a very small prosternal process, and anophthalmy and flightlessness as well. These are small dytiscids (total length = 1.25mm).

Classification. Brancucci (1985b) thought that certain features of these beetles suggest affinity with Bidessini (the shape of the metacoxal process and metatibiae), but also thought the shape of the prosternal process, in particular, is similar to *Kuschelhydrus* and *Phreatodessus*, the hypogean genera endemic to New Zealand.

Diversity. There is a single species in the genus, *T. monteithi* Brancucci.

Fig. 23.17. *Typhlodessus monteithi*. Scale = 1.0mm. Photo © Geoff Thompson, Queensland Museum, Brisbane, Australia, used with permission.

Natural History. *Typhlodessus* adults are terrestrial and have been collected in high-altitude rainforest (1,300–1,600m elevation) in moss and litter (Brancucci, 1985b). Additional details about the habitat and collection of the single known specimen were provided by Brancucci and Hendrich (2010).

Distribution. *Typhlodessus* are known only from New Caledonia (Map 23.4).

Map 23.4. Distribution of *Typhlodessus*.

24. Tribe Laccornini

Body Length. 3.3–7.2mm.

Diagnosis. Within Hydroporinae this group is characterized by a number of plesiomorphic features, including: (1) the metacoxal lobes large and apically rounded (Fig. 24.1); (2) the metafemur extending to the metacoxal lobe along the anterior margin and not separated from it by the metatrochanter (Fig. 24.1); and (3) the female with laterotergites present (Fig. 24.2). Specimens are typically brown to black with no markings (Fig. 24.3). They are very generalized Hydroporinae. Laccornini are difficult to diagnose externally from Laccornellini. The main difference is lack of laterotergites in Laccornellini (see Fig. 25.3), and their presence in Laccornini (Fig. 24.2), but this requires dissection.

Classification. *Laccornis* was historically placed near *Hydroporus* (e.g., Fall 1923; 1937), but Wolfe (1985; 1988) and Wolfe and Roughley (1990), based in part on characters of the female genitalia, among other features, hypothesized that *Laccornis* is sister to all the rest of Hydroporinae. Wolfe and Roughley (1990) erected a new tribe to include it. This has been corroborated by subsequent analyses based on larvae (Alarie, 1989) and molecular data (Miller and Bergsten, 2014a), though other analyses have suggested alternative topologies (Ribera *et al.*, 2008). However, a consensus is building that Laccornini is monophyletic and sister to most or all the other Hydroporinae.

Diversity. *Laccornis* is the only genus in the tribe.

Natural History. See below under *Laccornis*.

Distribution. See below under *Laccornis*.

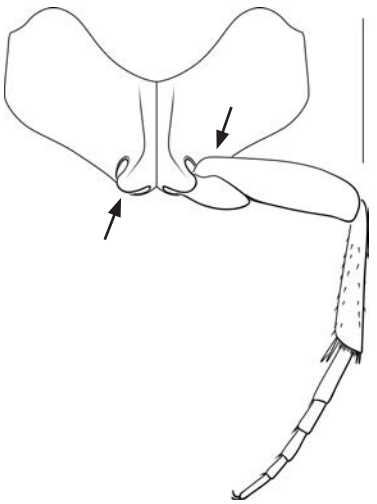


Fig. 24.1. *Laccornis oblongus*, metacoxa and left metaleg. Scale = 1.0mm.

Fig. 24.2. *Laccornis oblongus* female reproductive tract, ventral aspect. Scale = 1.0mm.

Genus *Laccornis* Gozis, 1914

Diagnosis. This is the only genus in the tribe, and it is characterized by its diagnosis (see above). Most species are small to moderately small, elongate oval, and dorsally brown to dark brown (Fig. 24.3).

Classification. See above for discussion of classification of the single genus, *Laccornis*.

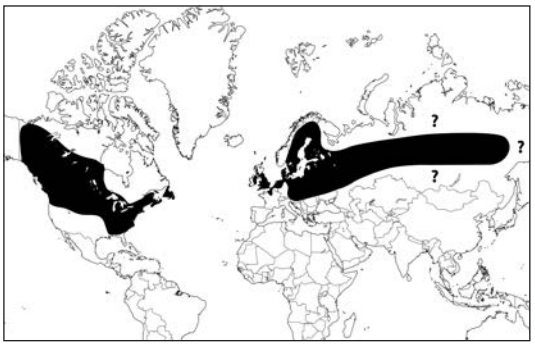
Diversity. The genus includes 10 species, most of which are Nearctic. The group was revised by Fall (1923; 1937) and Leech (1940) with modern, more comprehensive treatments by Wolfe and Spangler (1985) and Wolfe and Roughley (1990).

Natural History. *Laccornis* are found in forest pools, boreal bogs, and small lentic habitats. Larvae were described by Alarie (1989) and Cuppen and Dettner (1987).

Distribution. This is a Holarctic genus with one

Fig. 24.3. *Laccornis oblongus*. Scale = 1.0mm.

species found in both the Nearctic and Palearctic regions (Map 24.1). The eastern limits of the Palearctic species are poorly known.



Map 24.1. Distribution of *Laccornis*.

25. Tribe Laccornellini

Body Length. 1.7–4.6mm.

Diagnosis. Laccornellini are Hydroporinae species with the following character combination: (1) the metafemora extend to the metacoxal process (Fig. 25.1); (2) the metacoxal lobes are large and rounded (Fig. 25.1); (3) there is no oblique carina across the epipleuron at the humeral angle; (4) abdominal terga VII and VIII and elytra are apically evenly rounded (Figs. 25.4,5); and (5) the female genitalia lack laterotergites (Fig. 25.3). Two other characters were proposed by Roughley and Wolfe (1987): (1) the metacoxal process medially incised and (2) the sublateral row of the mesotibial spines sparse. These are difficult to homologize across Hydroporinae but do help to characterize Laccornellini. Laccornellini are difficult to diagnose externally from Laccornini. The main difference is lack of laterotergites in Laccornellini (Fig. 25.3), but this requires dissection.

Classification. Members of *Laccornellus* and *Canthyporus* have been historically placed in Hydroporini near *Laccornis* (Sharp, 1882; Zimmermann, 1919; 1920). Wolfe (1985; 1988) and Roughley and Wolfe (1987) suggested that *Laccornellus* and *Canthyporus* may be closely related to each other and together may be phylogenetically near Laccornini, Methlini, and Hydrovatini, which was corroborated by Ribera *et al.* (2008) and Shaverdo and Alarie (2006, based on larvae). Miller and Bergsten (2014a), however, found *Canthyporus* and *Laccornellus* to be sister groups and that clade sister to all Hydroporinae except Laccornini.

Diversity. Laccornellini includes two genera, *Canthyporus* and *Laccornellus*.

Natural History. Little is known of *Laccornellus* biology. Specimens have been collected in a small, temporary pond in *Nothofagus* forest (Roughley and Wolfe, 1987). *Canthyporus* have been found in highly vegetated pools, reservoirs, and occasionally in small springs, streams, and rivers (Biström and Nilsson, 2006).

Distribution. Members of this group occur in southern South America (*Laccornellus*) and southern and mountainous eastern Africa (*Canthyporus*).

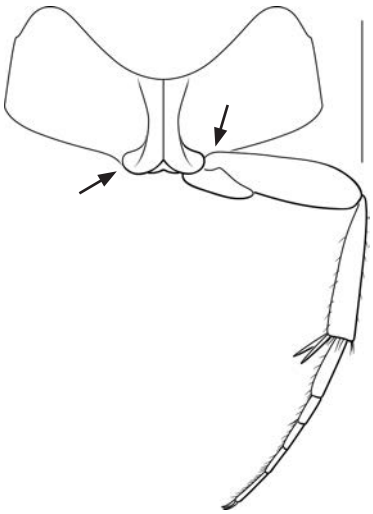


Fig. 25.1. *Laccornellus lugubris* metacoxae and left metaleg. Scale = 1.0mm.

Key to the Genera of Laccornellini

1 Apicolateral apex of elytron with short, broad, rounded bead (Fig. 25.2a); female gonocoxae complex, with two long lateral structures broadly fused by a bridge medially (Fig. 25.3a); size larger, length > 4.0mm; southern Neotropical (Map 25.2) . . . . *Laccornellus*, 148

1′ Apicolateral apex of elytron variable, most species with distinctive, curved carina (Fig. 25.2b), others with lower bead; female gonocoxae simple, not fused (Fig. 25.3b); size smaller, length < 4.0mm; Afrotropical (Map 25.1). . . . . *Canthyporus*, 148

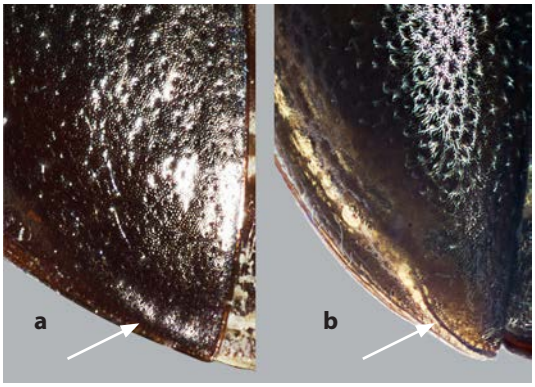


Fig. 25.2. Laccornellini, apicolateral apex of left elytron, oblique aspect. **a**, *Laccornellus lugubris*. **b**, *Canthyporus* sp.

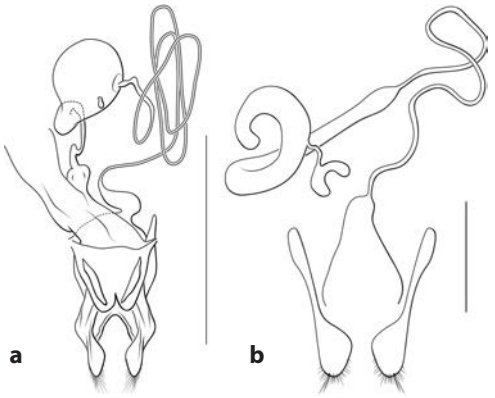


Fig. 25.3. Laccornellini female reproductive tract, ventral aspect. **a**, *Laccornellus copelatoides*. **b**, *Canthyporus hottentottus*. Scales = 1.0mm (a) and 0.25mm (b).

Genus *Canthyporus* Zimmermann, 1919

Body Length. 1.7–3.9mm.

Diagnosis. *Canthyporus* is difficult to differentiate from *Laccornellus*. There is a distinctive, curved, narrow carina or bead on the apicolateral margin of the elytron in many species, though some have this broader and lower, like in *Laccornellus* (Fig. 25.2b). The female gonocoxae are simple and not fused (Fig. 25.3b), but this requires dissection to determine. Roughley and Wolfe (1987) and Biström and Nilsson (2006) present few other features to differentiate them. See below under *Laccornellus* for details. Specimens are very small to small, elongate oval and evenly colored to variously patterned (Fig. 25.4).

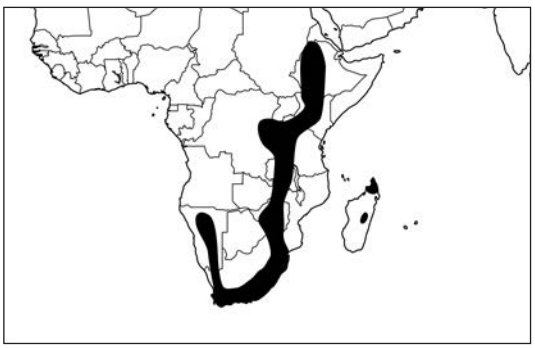
Classification. These species were originally placed in *Hydroporus* (e.g., Sharp, 1882; Régimbart, 1895) until placed in *Canthyporus* by Zimmermann (1919). Shaverdo and Alarie (2006) found *Canthyporus* sister to *Hydrovatus* and, importantly, well outside Hydroporini. They are sister to *Laccornellus*, and Miller and Bergsten (2014b) placed them together with that genus in Laccornellini.

Fig. 25.4. *Canthyporus hottentottus*. Scale = 1.0mm.

Diversity. There are currently 37 known species in *Canthyporus*. They are especially diverse in the Cape Region of South Africa (Biström and Nilsson, 2006). They were treated by several authors (Omer-Cooper, 1956; Bilardo and Sanfilippo, 1979; Wewalka, 1981; Nilsson, 1991; Mazzoldi, 1996) and completely revised by Biström and Nilsson (2006). Bilton (2015) treated the *C. exilis* group and described two new species.

Natural History. *Canthyporus* are found in highly vegetated pools, reservoirs, and in small springs, streams, and rivers (Biström and Nilsson, 2006). Some species are hygropetric and live in seepages on wet rock surfaces (Bilton, 2015). They occur at high elevation in northeastern Africa and Madagascar (e.g., >3,000m on Mount Kenya, Miller, unpublished, and >2,000m in Madagascar, Bergsten, unpublished). Larvae were described by Shaverdo and Alarie (2006).

Distribution. *Canthyporus* are known from southern Africa, mountainous areas north into Ethiopia, and (one species) from mountains in Madagascar (Map 25.1).



Map 25.1. Distribution of *Canthyporus*.

Genus *Laccornellus* Roughley and Wolfe, 1987

Body Length. 4.0–4.6mm.

Diagnosis. This genus is hard to differentiate from

Fig. 25.5. *Laccornellus lugubris.* Scale = 1.0mm.

Canthyporus. There is a broad, rounded bead at the apicolateral margin of the elytron (Fig. 25.2a), but at least some *Canthyporus* have a similar condition, and at least some *Laccornis* have something similar as well. The female gonocoxae are modified and broadly fused medially (Fig. 25.3a), but this requires dissection to examine. Roughley and Wolfe (1987) and Biström and Nilsson (2006) present a few other features to differentiate them, including the presence of a ligula on the ventral surface of the elytron and a short row of spines apically on the metafemur in *Canthyporus*, but these features have not been thoroughly surveyed to assess variation. Species are moderately large hydroporines, elongate, and brown (Fig. 25.5).

Classification. Species in this group were originally placed in *Hydroporus* (e.g., Sharp, 1882), and later in *Laccornis* (e.g., Wewalka, 1969; Wolfe, 1985), until placed in a new genus by Roughley and Wolfe (1987).

Diversity. There are currently two species, *L. copelatoides* (Sharp) and *L. lugubris* (Aubé).

Natural History. Specimens of *Laccornellus* were collected in a small, temporary pond in *Nothofagus* forest (Roughley and Wolfe, 1987). Larvae were described by Michat and Archangelsky (2013).

Distribution. This genus is known only from Chile and Argentina (Map 25.2).

Map 25.2. Distribution of *Laccornellus*.

26. Tribe Hydroporini

Body Length. 1.0–7.8mm.

Diagnosis. Hydroporini are Hydroporinae with (1) the metepisternum extending to the mesocoxal cavities (Fig. 26.1a); (2) the prosternal process extending to the metaventrite between the mesocoxae (Fig. 26.1a, except in a few taxa, including the North American *Stictotarsus minipi* (Larson) and several subterranean taxa); (3) the medial portion of the metacoxa in a different plane from the base of the abdomen (Fig. 26.1a); (4) the metacoxal lobes variable in shape but moderately large and prominent (Fig. 26.1a); (5) the metafemur along the dorsal margin broadly separated from the metacoxal lobes by the metatrochanter (Fig. 26.1a); (6) the apex of the elytra and the last abdominal segment not acuminate nor acutely pointed (Fig. 26.1a); (7) the metatarsal claws subequal in length (Fig. 26.1a); (8) the female genitalia with the laterotergites absent (Fig. 26.1b); and (9) the male lateral lobes of the aedeagus with a single segment (Fig. 26.1c).

Classification. This tribe historically included many Hydroporinae that are now classified in other tribes, including Laccornini, Hygrotini, many Bidessini, and, most recently changed, Laccornellini (Miller and Bergsten, 2014a). Even with these improvements, Hydroporini remains a difficult group to diagnose, and there are no really clear morphological synapomorphies. Several evidently monophyletic groups have been recognized within the tribe, including the *Deronectes*-group (J. Balfour-Browne, 1944; Nilsson and Angus, 1992; Angus and Tatton, 2011), the *Graptodytes*-group (Kuwert, 1890; Ribera *et al.*, 2002b; 2008; Ribera and Faille, 2010), the *Necterosoma*-group (Ribera *et al.*, 2002b; 2008), and the *Hydroporus*–group (Ribera *et al.*, 2002b; 2008). Each of these genus groups was found to be monophyletic by Ribera *et al.* (2008), but they were not together monophyletic in that analysis. All the Hydroporini taxa together and each of these groups were found to be monophyletic, however, in the analysis by Miller and Bergsten (2014a). They resurrected subtribe names for the four genus groups (Miller and Bergsten, 2014a). One genus, the subterranean *Siamoporus* Spangler, is placed in Hydroporini but is currently *incerta sedis* with respect to subtribe (see below and the key to subterranean genera).

Diversity. The tribe includes 4 subtribes and 38 genera. This is one of the largest tribes of Dytiscidae, and the generic classification has experienced considerable rearrangement and probably will continue to change.

Natural History. This group has a huge diversity of diving beetles with several groups characteristic of lentic habitats, others in lotic habitats, and a number of groups in seeps and springs. Some are in boreal

Fig. 26.1. Hydroporini features. **a,** *Hydroporus dichrous* ventral surface. **b,** *Nebrioporus dubius* female reproductive tract, ventral aspect. **c**, *Boreonectes striatellus* male genitalia, median lobe right lateral aspect, median lobe ventral aspect, lateral lobe. Scales = 1.0mm.

bogs and ponds, and others in the subtropics. Several species are subterranean. The group is difficult to generalize given its great diversity.

Distribution. This is a primarily Holarctic group with members absent from Central and South America, sub-Saharan Africa (largely), and southern and southeastern Asia. There is also a large radiation in the Australian region (Sternopriscina).

Key to the Subtribes of Hydroporini

1 Elytral epipleuron broad throughout length, not constricted medially and narrowed in apical half (Fig. 26.2a), or, if narrowed, then species found in Australia (genus *Paroster*, Fig. 26.2b). . . . . Sternopriscina, 180

1′ Elytral epipleuron not broad throughout length, constricted medially and narrowed throughout apical half (Fig. 26.2c), or broad throughout but found in the Palearctic (genus *Deronectes*, Fig. 26.2d) 2

2(1) Metacoxal process posteriorly either truncate, sinuate or medially angulate (projecting) (Fig. 26.3a-d) but not medially emarginate . . . . . Hydroporina, 154

2′ Metacoxal process medially emarginate (Fig. 26.3e). 3

3(2) Each side of lateral surface of pronotum with longitudinal impressed line (Fig. 26.4a,b). . . 4

3′ Each side of lateral surface of pronotum without longitudinal impressed line (Fig. 26.4c) . 6

4(3) Ventral surface densely shagreened, matte, and opaque (Fig. 26.5a) 5

4′ Ventral surface shiny, in some cases microreticulate (Fig. 26.5b), but not shagreened or matte . . . . . Siettitiina, in part, 172

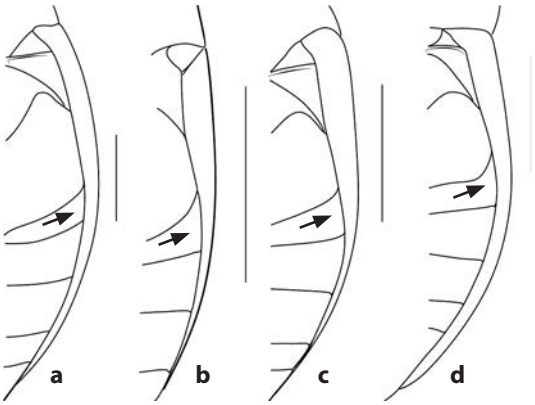


Fig. 26.2. Hydroporini left elytral epipleuron. **a**, *Chostonectes gigas*. **b**, *Paroster pallescens*. **c**, *Hydroporus dichrous*. **d**, *Deronectes depressicollis*. Scales = 1.0mm.

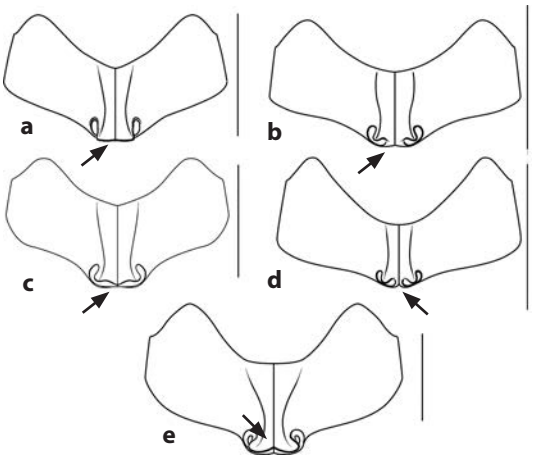


Fig. 26.3. Hydroporini metacoxae. **a**, *Hydroporus dichrous*. **b**, *Heterosternuta wickhami*. **c**, *Neoporus dimidiatus*. **d**, *Sanfilippodytes sp*. **e**, *Deronectes depressicollis*. Scales = 1.0mm.

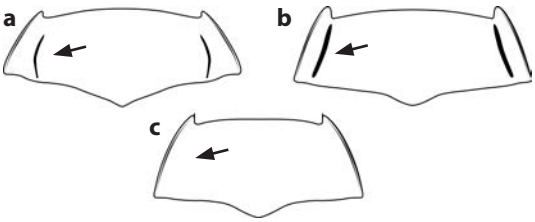


Fig. 26.4. Hydroporini pronota. **a**, *Oreodytes quadrimaculatus*. **b**, *Rhithrodytes sexguttatus*. **c**, *Lioporeus triangularis*.

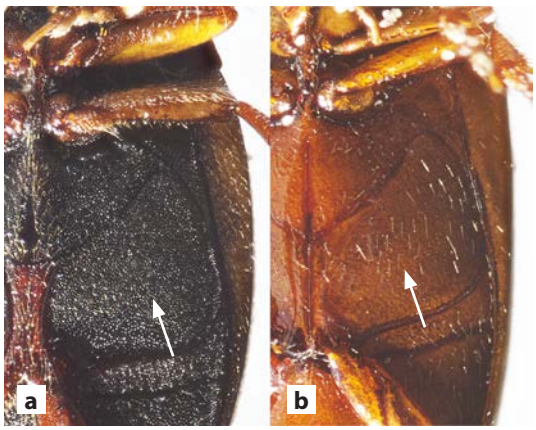


Fig. 26.5. Hydroporini ventral surfaces. **a**, *Stictonectes optatus*. **b**, *Rhithrodytes sexguttatus*..

5(4) Apical labial palpomere not distinctly bifid (Fig. 26.6a); antennomere IV only slightly narrower than others (Fig. 26.7a)
. . . . . Deronectina, *Oreodytes*, 168

5′ Apical labial palpomere distinctly bifid (Fig. 26.6b); antennomere IV conpicuously smaller than others (Fig. 26.7b)
. . . . . .Siettitiina, *Stictonectes*, 178

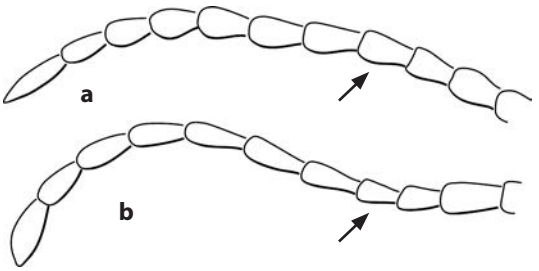


Fig. 26.7. Hydroporini left antenna. **a**, *Oreodytes alpinus*. **b**, *Stictonectes optatus*.

6(3) Ventral surface densely shagreened, matte, and opaque, or shiny and punctate (Fig. 26.8a), but not microreticulate; total length > 3mm
. . . . . Deronectina, in part, 162

6′ Ventral surface shiny and microreticulate (Fig. 26.8b); total length < 3mm
. . . . . Siettitiina, *Metaporus*, 175

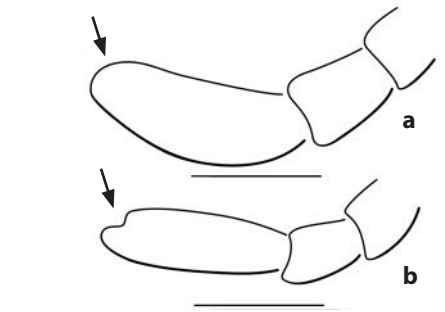


Fig. 26.6. Hydroporini labial palpi. **a**, *Oreodytes laevis*. **b**, *Stictonectes optatus*. Scales = 0.1mm.

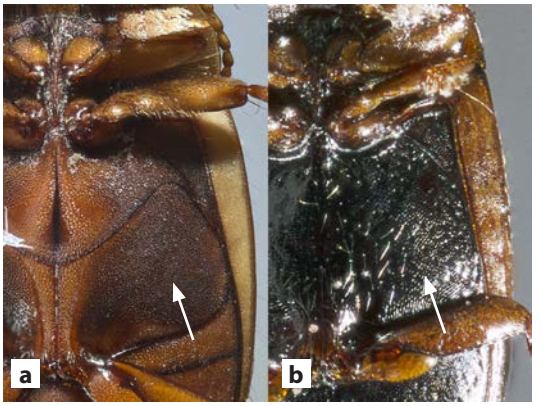


Fig. 26.8. Hydroporini ventral surfaces. **a**, *Nebrioporus assimilis*. **b**, *Metaporus meridionalis*.

Fig. 26.9. *Siamoporus deharvengi*. Scale = 1.0mm.

Genus *Siamoporus* Spangler, 1996

Body Length. 3.2–3.6mm.

Diagnosis. The one species in *Siamoporus* is characterized by typical stygobitic phenotypes: depigmentation, absence of eyes, flightlessness, and a

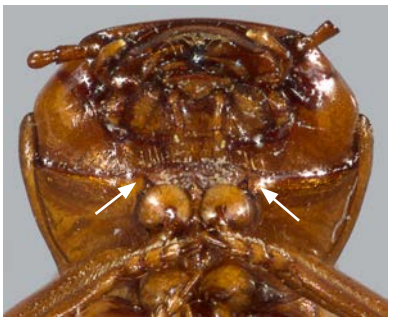


Fig. 26.10. *Siamoporus deharvengi* head and prothorax, ventral aspect.

distinctly cordate pronotum (Fig. 26.9). There are numerous other species in the tribe that are stygobitic, and this one is difficult to diagnose from them. However, the apices of the elytra in *Siamoporus* are subtruncate (Fig. 26.9), and there are distinctive short, tectiform carinae on each side of the prosternum (Fig. 26.10).

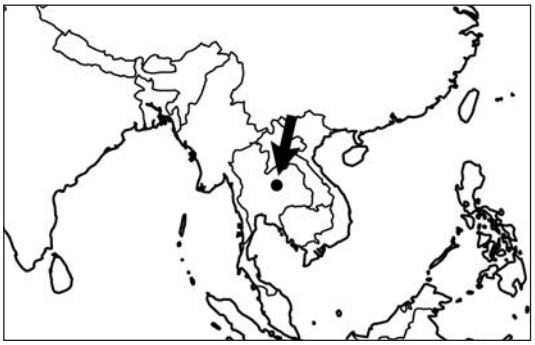
Classification. Spangler (1996) placed this genus in Hydroporini, but it may be only uncomfortably placed in the tribe, and there is no clear evidence regarding its placement in any of the subtribes recognized here. It is here regarded as *incerta sedis*

with respect to subtribe, and its relationships, like many stygobitic species known only from morphology, are obscure.

Diversity. There is a single species, *S. deharvengi* Spangler.

Natural History. Specimens were collected from a cave in clear water with numerous other animals, including isopods, amphipods, and planarians (Spangler, 1996).

Distribution. *Siamoporus deharvengi* is known only from the type locality, a cave in Khon Khen Province, Thailand (Map 26.1).



Map 26.1. Distribution of *Siamoporus*.

27. Subtribe Hydroporina

Body Length. 1.8–6.4mm.

Diagnosis. These are Hydroporini with a number of absence characters, internal features, or apparent plesiomorphies, including: (1) the elytral epipleuron abruptly narrowed medially, and narrow throughout the apical half (Fig. 27.1a); (2) the transverse tooth of the proventriculus not apically shallowly multilobed; (3) the mesosternal fork and the anteromedial process of the metaventrite not connected; (4) receptacle on the spermathecal duct, not on the female bursa (Fig. 27.1b); and (5) the rami of the female genitalia variously shaped but not elongate curved nor apically fused together (Fig. 27.1b),

Classification. This group of genera is monophyletic in the analyses by Ribera *et al.* (2002b; 2008), who recognized the clade as the "*Hydroporus*-group" of genera. The clade was recognized as as a well-supported formal subtribe of Hydroporini by Miller and Bergsten (2014a), though really good morphological synapomorphies are not evident.

Diversity. Seven genera are now included in this subtribe after *Stygoporus* was transferred to Siettitiina.

Natural History. This diverse group occurs in many habitats, especially boreal pools, including *Sphagnum* bogs and forest ponds. Some are the most northerly occurring diving beetles, well into the Arctic (see *Hydroporus* below).

Distribution. This a Holarctic group with members distributed across North America, Europe, and northern Asia.

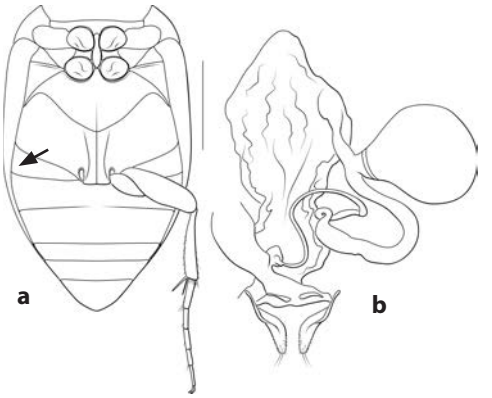


Fig. 27.1. Hydroporina features. **a**, *Hydroporus dichrous* ventral surface. **b**, *H. notabilis* female genitalia, ventral aspect. Scale = 1.0mm..

Key to the Epigean Genera of Hydroporina

One genus in Hydroporina, *Haideoporus*, is subterranean in Texas, USA. It has features typical of subterranean diving beetles (Fig. 3.51, flightless, eyeless, depigmented) and is keyed separately in the key to subterranean taxa (page 45).

1 Posterior margin of metacoxal process straight or angulate medially, not medially emarginate or sinuate (Fig. 27.2a,b). 2

1′ Posterior margin of metacoxal process sinuate medially (Fig. 27.2c,d) 3

2(1) Posterior margin of metacoxal process straight to slightly angulate medially (Fig. 27.2a); ventral surface of most specimens black or mostly black with few red maculae; Holarctic (Map 27.4) . . . . . *Hydroporus*, 157

2′ Posterior margin of metacoxal process strongly angulate medially (Fig. 27.2b); ventral surface of most specimens pale yellow to red; Nearctic (Map 27.6) . . . . . *Neoporus* (in part), 159

3(1) Metatrochanter large, metafemur about 1.9–2.2 × length of metatrochanter (Fig. 27.2c); Nearctic (Map 27.7). . . . .*Sanfilippodytes*, 160

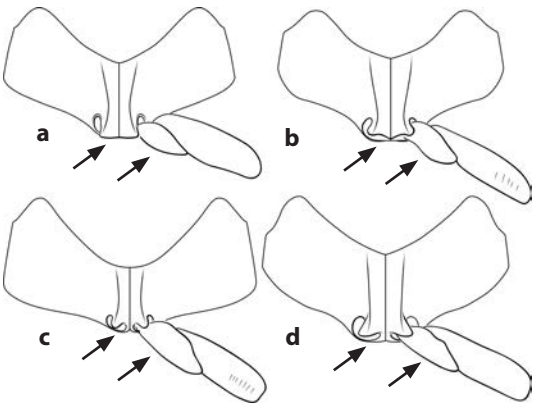


Fig. 27.2. Hydroporina metacoxae. **a**, *Hydroporus dichrous*. **b**, *Neoporus dimidiatus*. **c**, *Sanfilippodytes* sp. **d**, *Lioporeus triangularis*.

3′ Metatrochanter shorter, metafemur about 2.3–2.8 × length of metatrochanter (Fig. 27.2d). . 4

4(3) Apex of scutellum visible with elytra closed (Fig. 27.3b); elytra without maculae (Fig. 27.10); male protibia with large basoventral emargination (Fig. 27.4a); Nearctic and northern Palearctic (Map 27.3) . . . . . .*Hydrocolus*, 157

4′ Entire scutellum hidden with elytra closed (Fig. 27.3b); elytra with maculae or fasciae; male protibia not emarginate (Fig. 27.4b) . . . 5

5(4) Prosternal process without basal protuberance (Fig. 27.5a); male antennomere V or V and IV laterally expanded (Fig. 27.12); male protarsomere I with basoventral cup-shaped collection of many adhesive setae (Fig. 27.6a); eastern Nearctic (Map 27.5) . . *Lioporeus*, 159

5′ Prosternal process with basal protuberance (Fig. 27.5b); male antennomeres V and IV unmodified; male protarsomere I without basoventral cup-shaped collection of many adhesive setae (Fig. 27.6b) 6

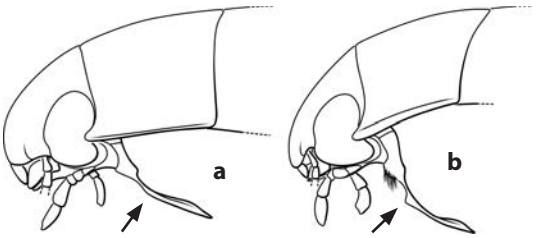


Fig. 27.5. Hydroporina, lateral aspect. **a**, *Lioporeus triangularis*. **b**, *Heterosternuta wickhami*.

6(5) Male median lobe apically bifid (Fig. 27.7a); elytra without narrow longitudinal lines . . . . . .*Heterosternuta*, 156

6′ Male median lobe apically entire (Fig. 27.7b); elytra with narrow lontitudinal lines . . . . . *Neoporus* (in part) *shermani*, 159

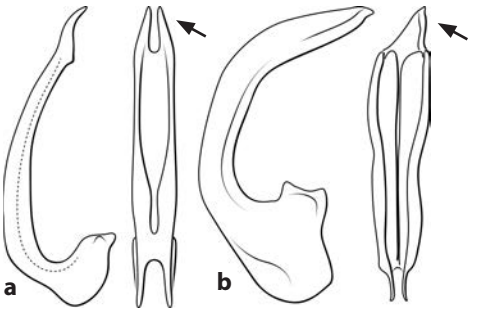


Fig. 27.7. Hydroporina male median lobe right lateral and ventral aspects. **a**, *Heterosternuta cocheconis*. **b**, *Neoporus shermani*.

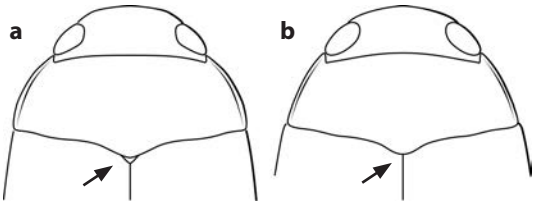


Fig. 27.3. Hydroporina, dorsal surface. **a**, *Hydrocolus paugus*. **b**, *Heterosternuta wickhami*.

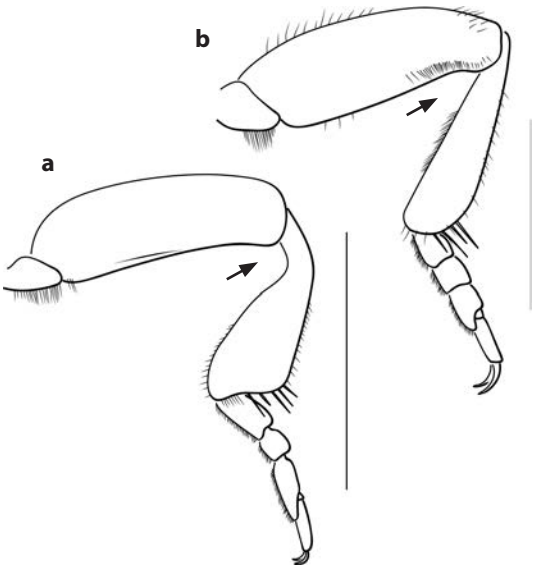


Fig. 27.4. Hydroporina male prolegs. **a**, *Hydrocolus rubyi*. **b**, *Heterosternuta wickhami*. Scales = 1.0mm.

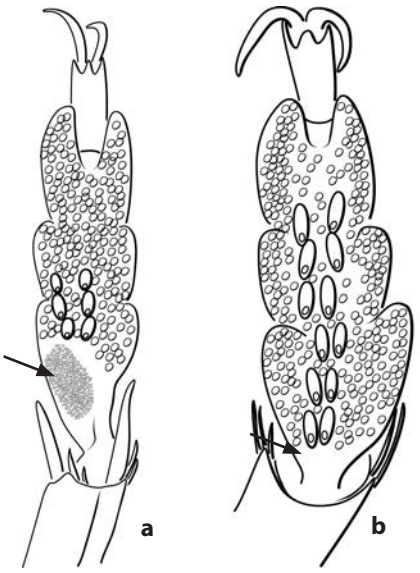


Fig. 27.6. Hydroporina male protarsi, ventral surface. **a**, *Lioporeus triangularis*. **b**, *Heterosternuta wickhami*.

Fig. 27.8. *Haideoporus texanus*. Scale = 1.0mm.

Genus *Haideoporus* Young and Longley, 1976

Body Length. 3.4–3.7mm.

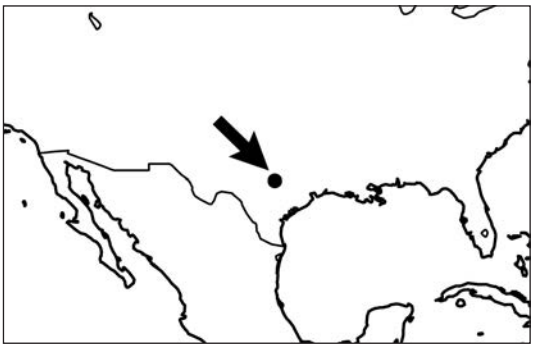
Diagnosis. This genus is stygobitic and has the eyes absent, is depigmented, has fused elytra, and other typical features of subterranean taxa (Fig. 27.8). *Haideoporus* has natatory setae unlike many other stygobionts.

Classification. The genus is closely related to *Heterosternuta* and *Neoporus* (Miller *et al.*, 2013; Miller and Bergsten, 2014a).

Diversity. There is only a single species in the genus, *Haideoporus texanus* Young and Longley. The genus was reviewed, along with other North American stygobionts, by Miller *et al.* (2009b).

Natural History. *Haideoporus texanus* is subterranean in the Edwards-Trinity Aquifer in central Texas. The larvae have been described by Longley and Spangler (1977) and Alarie *et al.* (2013).

Distribution. In addition to the type locality, the species was reported by Bowles and Stanford (1997) from an artesian borehole in San Marcos, Texas. This species is now known from several springs within about a 30mi radius that emerge from the southern margin of the Edwards-Trinity Aquifer of central Texas (Map 27.1). Several additional subterranean diving beetles are also known from these springs.



Map 27.1. Distribution of *Haideoporus*.

Genus *Heterosternuta* Strand, 1935

Body Length. 2.6–4.6mm.

Diagnosis. Members of this group have the posterior margin of the metacoxal process laterally sinuate (as in Fig. 27.2d), the scutellum entirely hidden (Figs. 27.3b,9), the protibia not emarginate (Fig. 27.4b), the prosternal process with a distinctive basal protuberance (Fig. 27.5b), the male antennae not modified (Fig. 27.9), and the male median lobe apically bifid (Fig. 27.7a). Members of the group are ventrally red to black, and dorsally most species are attractively maculate or fasciate (Fig. 27.9).

Classification. This group was recognized together with other genera in a much larger *Hydroporus* as the *H. pulcher* (=*H. pulchra*) portion of the *Hydroporus pulcher-undulatus* group (Fall, 1923). Zimmermann (1919) erected *Hydroporus* (*Heterosternus*) Zimmermann (replaced with *H.* (*Heterosternuta*) Strand) for the group, and it was recognized that way until recently (e.g., Matta and Wolfe, 1981). Alarie and Nilsson (1997) elevated it to genus rank. The genus is closely related to *Neoporus* (Ribera *et al*., 2008; Miller and Bergsten, 2014a).

Diversity. There are currently 14 species in the genus, and they were revised by Matta and Wolfe

Fig. 27.9. *Heterosternuta pulchra*. Scale = 1.0mm.

(1981) and recently treated by Larson *et al.* (2000).

Natural History. Members of *Heterosternuta* are primarily lotic and found especially in small streams, seeps, and springs or gravel margins of lakes and ponds. Larvae have been described by Alarie (1992) and Alarie and Fritz (1998).

Distribution. *Heterosternuta* occur in eastern North America (Map 27.2).

Map 27.2. Distribution of *Heterosternuta*.

Genus *Hydrocolus* Roughley and Larson, 2000

Body Length. 2.6–4.7mm.

Diagnosis. *Hydrocolus* are characterized by: (1) the posterior margin of the metacoxal process distinctly sinuate (as in Fig. 27.2d); (2) the metatrochanter relatively small with the metafemur about 2.3–2.8 × the length of the metatrochanter (as in Fig. 26.2d); (3) portions of the scutellum visible with the elytra closed (Fig. 27.3a,10); and (4) males with the protibia emarginate along the ventral margin (Fig. 27.4a). Members of the group are concolorous dorsally without distinctive maculae or fasciae (Fig. 27.10).

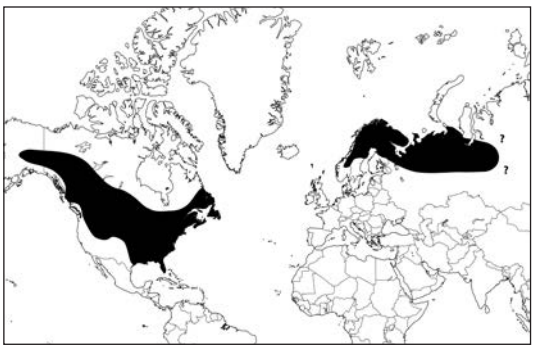
Fig. 27.10. *Hydrocolus paugus*. Scale = 1.0mm.

Classification. This genus corresponds to the *Hydroporus oblitus* group of species of Fall (1923). *Hydrocolus* was erected for the group by Roughley and Larson (in Larson *et al.*, 2000). *Hydrocolus* is likely closely related to *Hydroporus* (Ribera *et al.*, 2008; Miller and Bergsten, 2014a).

Diversity. There are 12 species currently assigned to *Hydrocolus*, and they have been revised by Roughley and Larson (in Larson *et al.*, 2000) with a new species described by Ciegler (2001).

Natural History. Many species of *Hydrocolus* occur in wet mosses along the margins of seeps and springs with others in more typical habitats like bogs, marshes, or sandy streams. At least one species is known from monadnock (inselberg) habitats (Ciegler, 2001), suggesting that other hygropetric habitats should be investigated more thoroughly for additional species.

Distribution. Most species occur in eastern North America, with a couple in western North America and a single species in the northern Palearctic from Fennoscandia to east Siberia (Map 27.3).



Map 27.3. Distribution of *Hydrocolus*.

Genus *Hydroporus* Clairville, 1806

Body Length. 1.9–7.1mm.

Diagnosis. *Hydroporus* includes Hydroporina species with the posterior margin of the metacoxal process straight, without sinuation or emargination (Fig. 27.2a), but sometimes slightly angulate. *Hydroporus* species are variable, but most are brown to reddish-black to black (Fig. 27.11a,b), and some

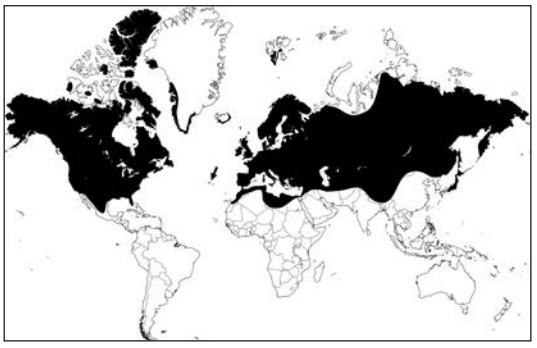
Fig. 27.11. *Hydroporus* species. **a**, *H. planus*. **b**, *H. tristis*. **c**, *H. figuratus*. Scales = 1.0mm.

have distinct pale fascia or maculae (Fig. 27.11c).

Classification. This is a large group that historically included many taxa now in other genera (Fall, 1923). Historically, *Suphrodytes* Gozis was treated as a species group or subgenus of *Hydroporus* (e.g., F. Balfour-Browne, 1934c). Angus (1985) argued for recognition of the group at the genus rank separate from *Hydroporus*. This common European group has had a long history of taxonomic study, with many species names associated with it based in part on the highly variable coloration, size and shape of specimens (e.g., Zimmermann, 1919). Recently Bergsten *et al.* (2012) undertook a comprehensive examination of the morphology and DNA sequence data in *Suphrodytes* and discovered two broadly sympatric species. *Suphrodytes* was then also synonymized with *Hydroporus* by Bergsten *et al.* (2013). Also, three madicolous species in Macaronesia were previously treated in the separate genus, *Hydrotarsus* Falkenström, which was synonymized with *Hydroporus* by Ribera *et al.* (2003a). *Hydroporus* has been divided into numerous species groups (Nilsson, 2001), and their relationships have been studied with molecular data by Ribera *et al.* (2003a), Hernando *et al.* (2012) and Bergsten *et al.* (2013).

Diversity. *Hydroporus* currently includes 188 species, making it one of the largest diving beetle genera. The New World taxa were revised by Fall (1923), and in part by Gordon (1969; 1981) and Larson (1975), but more recently by Larson *et al.* (2000). Old World taxa have been revised by numerous authors (e.g., Zimmermann, 1931; F. Balfour-Browne, 1934c; Zaitzev, 1953; Wewalka, 1971; 1992; Foster and Angus, 1985; Nilsson and Nakane, 1992; Balke and Fery, 1993; Nilsson, 1994a; Fery, 1999; Shaverdo, 2004; 2006). Nearctic species are extremely difficult to identify, as are some species groups in the Palearctic. Nevertheless, this is a commonly encountered group of relatively homogeneous species.

Natural History. This large group has many common North American and European members, and, as such, much more is known about *Hydroporus* biology and ecology than other dytiscid groups. Members of the group are found in a variety of habitats from boreal bogs and fens to streams, seeps, and springs. At least some are found in interstices in the substrate (Hernando *et al.*, 2012). *Hydroporus morio* Aubé and *H. polaris* Fall occur at remarkably high northern latitudes (Jeppesen, 1986; Böcher, 1988; Debruyn and Ring, 1999; Larson *et al.*, 2000), in at least some cases in warm springs (Heide-Jorgensen and Kristensen, 1999). Having been found at over 80°N latitude, these are the most northerly occurring diving beetles. Larvae have been described by Jeppesen (1986), Nilsson (1986a; b; 1989a), Nilsson and Carr (1989), Alarie (1991; 1992; 1995a), Shaverdo (2000a; b), Alarie and Bilton (2001), and Alarie *et al.* (2001c). Their flight and migration behavior and other life history information were



Map 27.4. Distribution of *Hydroporus*.

investigated by Behr (1990; 1992; 1993a; b; 1994; 1995). Distribution ecology and other aspects of life history, mainly of *H. glabriusculus* Aubé, were also treated by Bilton (1992; 1993a; b; 1994a; b). Other aspects of *Hydroporus* biology and ecology were investigated by several authors (Matheson, 1914; Jackson, 1958b; Cuppen, 1986; Gilbert, 1986; Juliano, 1991; Boltin, 1992; Nilsson, 1997; Debruyn and Ring, 1999; Lundkvist *et al.*, 2002; Sueselbeck, 2002a; b). At least one species has been described as "semi-subterranean" (Manuel, 2013).

Distribution. *Hydroporus* occur throughout the Holarctic south into Mexico and northern Africa (Map 27.4). Several species are Holarctic. This group includes the most northerly occurring diving beetles with *H. morio* and *H. polaris* Fall each found in the Arctic to about 80°N (Map 27.4).

Genus *Lioporeus* Guignot, 1950

Body Length. 3.4–4.4mm.

Diagnosis. *Lioporeus* are Hydroporina with male antennomeres V or V and IV laterally expanded (Fig. 27.12), the posterior margins of the metacoxal process sinuate and laterally emarginate (Fig. 27.2d), the metatrochanter relatively short with the metafemur about 2.3–2.8 × the length of the metatrochanter (Fig. 27.2d), the male protibia not emarginate (as in Fig. 27.4b), and the prosternal process does not have a basal protuberance (Fig. 27.5a). Males have a small cluster of dense adhesive setae ventrally on protarsomere I (Fig. 27.6a). The species in this group are elongate and dorsally maculate (Fig. 27.12).

Fig. 27.12. *Lioporeus pilatei*. Scale = 1.0mm.

Classification. These species were part of the *Hydroporus pulcher-undulatus* group of Fall (1923). Wolfe and Matta (1981) rearranged the classification, erecting a new genus, *Falloporus* Wolfe and Matta, to include two species. This name was later synonymized with *Lioporeus* Guignot (Wolfe, 1983). The genus has not been included in recent phylogenetic analyses, and nothing is yet known about its relationships with other taxa.

Diversity. There are two species placed in *Lioporeus*, *L. triangularis* (Fall) and *L. pilatei* (Fall), which can be identified with Larson *et al.* (2000).

Natural History. *Lioporeus* occur along the margins of small, clear streams.

Distribution. This genus is found in eastern North America (Map 27.5).

Map 27.5. Distribution of *Lioporeus*.

Genus *Neoporus* Guignot, 1931

Body Length. 2.3–6.4mm.

Diagnosis. Within Hydroporina, *Neoporus* are distinctive in having the posterior margin of the metacoxal process projected medially in an angle with the lateral margins not sinuate or otherwise emarginate (Fig. 27.2b). Most species are maculate or fasciate dorsally (Fig. 27.13) and yellow to red on all ventral surfaces, though some have the dorsal and ventral surfaces very dark or nearly black.

Classification. This group was long placed together with other genera in a larger *Hydroporus* as the *H. undulatus* portion of the *Hydroporus pulcher-undulatus* group (Fall, 1923). After Guignot (1931) erected *Neoporus* as a subgenus of *Hydroporus* for this subgroup, it was usually recognized as a subgenus (e.g., Wolfe, 1984) until elevated by Alarie and Nilsson (1997). The genus has historically been regarded as closely related to *Heterosternuta* (Fall, 1923; Ala-

Fig. 27.13. *Neoporus* species. **a**, *N. dimidiatus*. **b**, *N. tennetum*. Scales = 1.0mm.

rie and Nilsson, 1997; Wolfe, 1984), a conclusion supported also by recent, larger cladistic analyses (Ribera *et al.*, 2008; Miller and Bergsten, 2014a).

Diversity. There are currently 39 species in this large genus. Wolfe (1984) revised a subgroup, the *N. vittatipennis* group, and Larson *et al.* (2000) keyed and diagnosed all the species, though the entire group is in need of revision since many species are similar and there seem likely to be undescribed species.

Natural History. Members of the group occur in both lentic and lotic habitats, depending on the species, with some in ponds and lakes, the margins of rivers and streams, and seeps and springs. They often come to lights. Larvae were described by Matta and Peterson (1985), Scott *et al.* (2004), and Alarie (1991).

Distribution. The greatest diversity of species occur in the eastern United States with fewer in northern and western North America south into northern Mexico (Map 27.6).

Map 27.6. Distribution of *Neoporus*.

Genus *Sanfilippodytes* Franciscolo, 1979

Body Length. 2.1–4.3mm.

Diagnosis. *Sanfilippodytes* have the following combination within Hydroporina: (1) the posterior margin of the metacoxal process distinctly sinuate (Fig. 27.2c) and (2) the metatrochanter relatively large with the metafemur about 1.9–2.2 × the length of the metatrochanter (Fig. 27.2c). Members of the group are characteristically concolorous dorsally without maculae or fasciae (Fig. 27.14), though many species have the pronotum and/or the bases of the elytra darker than the rest of the elytra, making them distinctly bicolored.

Classification. This group corresponds to the *Hydroporus vilis* group of Fall (1923). The genus was originally erected for a putative cave species, *S. sbordonii* Franciscolo, from Mexico (Franciscolo, 1979b;

Fig. 27.14. *Sanfilippodytes kingii*. Scale = 1.0mm.

1983). This species was regarded as typical of the *H. vilis* group, and *Sanfilippodytes* was used for the entire group by Larson *et al.* (2000), as suggested by Rochette (1983), Roughley and Larson (1991), and Larson and Labonte (1994). How *Sanfilippodytes* is related to other Hydroporina genera is uncertain.

Diversity. There are 25 species currently assigned to the genus as listed by Rochette (1983). They were keyed by Larson *et al.* (2000), but as they indicate, this is an extremely difficult group that needs considerable, comprehensive revisionary work to clarify species limits and delimitations.

Natural History. *Sanfilippodytes* are characteristic of small seeps and springs, margins of streams, and mineral substrates along margins of alpine lakes. At least one species has been found in a cave, though it is not entirely clear that the species is subterranean (Franciscolo, 1979a; 1983).

Distribution. Most species are found in the western United States from Alaska south into Mexico, but a few extend east to Labrador and Newfoundland (Map 27.7).

Map 27.7. Distribution of *Sanfilippodytes*.

28. Subtribe Deronectina

Body Length. 2.4–7.8mm.

Diagnosis. This group differs from other Hydroporini in at least three somewhat obscure morphological synapomorphies: (1) the transverse tooth of the proventriculus is apically shallowly multilobed (Fig. 28.2; Miller *et al.*, 2006); (2) the rami of the female genitalia are characteristically shaped, elongate curved, apically fused, and together apically rounded (Fig. 28.1, Miller, 2001c; Miller *et al.*, 2006); and (3) the mesosternal fork and anteromedial process of the metaventrite are not connected (Nilsson and Angus, 1992). Unfortunately, each of these features is (more or less) internal and therefore difficult to assess for diagnostic purposes (and taxa have not been comprehensively surveyed for these attributes). Potentially diagnostic external features are much more variable across the subtribe and overlap with taxa in other subtribes. Species differ from Sternopriscina in having the elytral epipleuron abruptly narrowed in the apical half, except *Deronectes*, which have the epipleuron wide throughout most of their length, but which do not live in the Australian region. In general, most deronectines have the ventral surface covered with shagrination or dense punctation, but some have microreticulation or are shiny and sparsely punctate. Deronectines lack an impressed line longitudinally on each side of the pronotum, except *Oreodytes*. Members of *Oreodytes* also have the male pro- and mesotarsomeres I–III with ventral adhesive setae (Fig. 28.4a), but the rest of Deronectina do not have adhesive setae on the mesotarsomeres (Fig. 28.4b). At least some of the Australian Sternopriscina have a similar condition (Nilsson and Angus, 1992). The status of some of these attributes was discussed recently by Fery and Petrov (2013).

Classification. Deronectina corresponds to the *Deronectes* group of genera of other authors (J. Balfour-Browne, 1944; Nilsson and Angus, 1992; Angus and Tatton, 2011). *Oreodytes* is not always included within that group (e.g., Nilsson and Angus, 1992; Angus, 2010a) since they have the abovementioned character state differences from the other genera. Most investigators have generally agreed, however, that Oreodytes is at least related to, and possibly the sister group of, the other genera (e.g., Fery and Petrov, 2013, but see phylogeny in Miller and Bergsten, 2014a and Ribera *et al*., 2008). J. Balfour-Browne (1944) addressed the complicated genus-group classification, but the most comprehensive examination in modern times was by Nilsson and Angus (1992), who synonymized, elevated and reconstituted several genus-groups and provided diagnoses. In modern analyses, Ribera *et al.* (2008) found the group, including *Oreodytes*, to be monophyletic. Miller and Bergsten (2014a) also found the group, again with *Oreodytes*, to be monophyletic with strong support. Despite these efforts, several of the genera and species groups are difficult to diagnose or are only subtly different, and new genera continue to be recognized (Angus, 2010a; Fery and Petrov, 2013). Some of the classification has emphasized karyotypic data (Nilsson and Angus, 1992; Angus, 2010a; Angus and Tatton, 2011). Guignot (1941) revised many of the taxa (as *Potamonectes* Zimmermann). Relationships with other groups are ambiguous, though Miller and Bergsten (2014a) found them sister to Siettitiina.

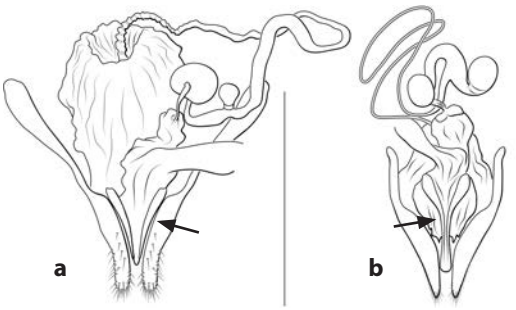


Fig. 28.1. Deronectina, female reproductive tract, ventral aspect. **a**, *Deronectes platynotus*. **b**, *Nebrioporus dubius*. Scales = 1.0mm.

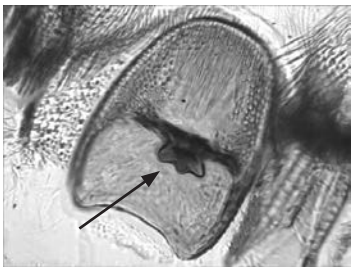


Fig. 28.2. *Scarodytes halensis* proventriculus crusher lobe.

Diversity. The subtribe includes eight genera. Because of the considerable similarity among taxa, it seems likely that additional future taxonomic rearrangment can be expected, and Deronectina remains in a taxonomic flux at the genus level.

Natural History. Most members of this group are distinctly stream inhabiting. They can be found in lentic habitats, but usually on mineral substrates from stream bottoms to shallow rock pools to margins of lakes. A number of studies of karyotypes have been done within this group. Several members of the group, including *Deronectes* and certain *Stictotar-*

sus, have XX/XY sex determination, but in others, including *Scarodytes*, *Nebrioporus*, *Trichonectes*, and *Boreonectes*, it is XX/XO (Nilsson and Angus, 1992; Angus, 2010a; Angus and Tatton, 2011).

Distribution. This is a primarily Holarctic group with some representatives extending south through Mexico and farther south through the mountains of Africa to South Africa (*Nebrioporus*).

Key to the Genera of Deronectina

1 Pronotum sublaterally with distinct longitudinal impression on each side (Fig. 28.3a); pro- and mesotarsomeres of males with ventral adhesive discs (Fig. 28.4a); Holarctic (Map 28.5). . . . . *Oreodytes*, 168

1' Pronotum sublaterally without distinct longitudinal impression on each side (Fig. 28.3b); pro- and mesotarsomeres of males without ventral adhesive discs (Fig. 28.4b) 2

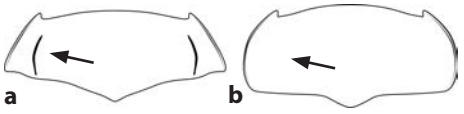


Fig. 28.3. Deronectina pronota. **a**, *Oreodytes quadrimaculatus*. **b**, *Nebrioporus assimilis*.

2(1) Dorsal surface concolorous red-brown to black or bicolored but not vittate or maculate (Fig. 28.19); metacoxal processes with interlaminary bridge exposed (Fig. 28.5a); metatibia with anterior surface covered with punctures (Fig. 28.6a); metatarsomere V about 2 × length of metatarsomere IV (Fig. 28.5a); Palearctic (Map 28.3). . . . . *Deronectes*, 166

2' Dorsal surface vittate or maculate (e.g., Fig. 28.20); metacoxal processes with interlaminary bridge mostly concealed in most species (Fig. 28.5b) or broadly exposed; metatibia with anterior surface with longitudinal row of spiniferous punctures (Fig. 28.6b), or, if covered with punctures, the interlaminary bridge is concealed; metatarsomere V about 1.5 × length of tarsomere IV (Fig. 28.5b). 3

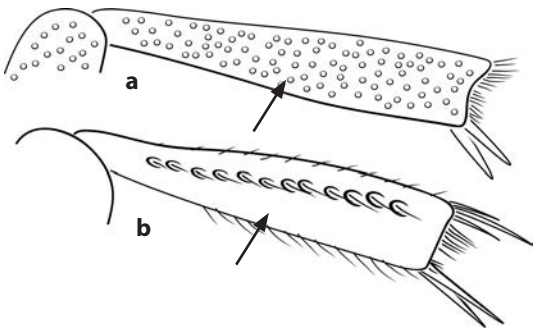


Fig. 28.6. Deronectina metatibia, ventral aspect. **a**, *Deronectes depressicollis*. **b**, *Nebrioporus carinatus*.

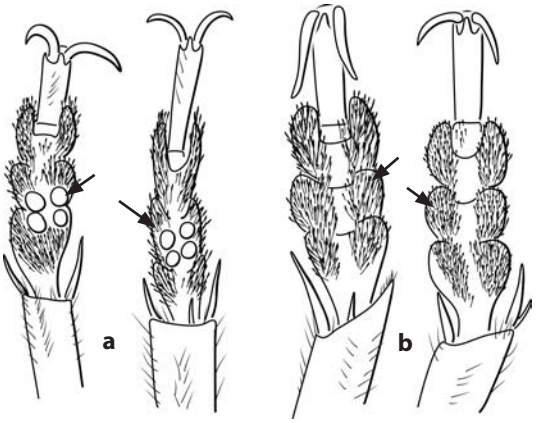


Fig. 28.4. Deronectina right protarsi and mesotarsi. **a**, *Oreodytes quadrimaculatus*. **b**, *Deronectes ferrugineus*.

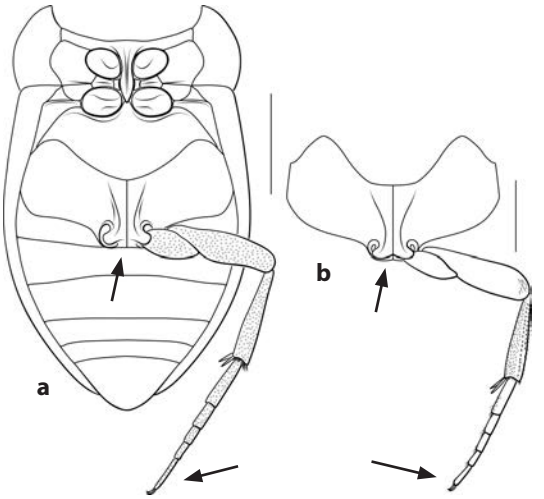


Fig. 28.5. Deronectina ventral surfaces. **a**, *Deronectes depressicollis*. **b**, *Nebrioporus canariensis*. Scales = 1.0mm.

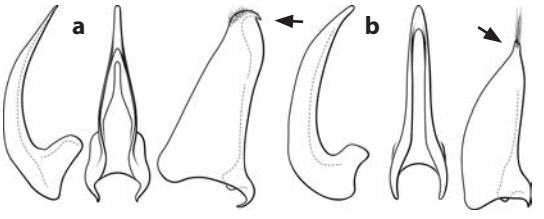


Fig. 28.7. Deronectina male genitalia, median lobe right lateral aspect, median lobe ventral aspect, right lateral lobe lateral aspect. **a**, *Nebrioporus elegans*. **b**, *Boreonectes striatellus*.

3(2) Male lateral lobe with apical sclerotized hook (Fig. 28.7a); elytron with subapical spine (Fig. 28.8a) or not (Fig. 28.8b); ventral surface densely punctate or shiny or microreticulate with sparse, coarse punctures (Fig. 28.9a) . . 4

3' Male lateral lobe without apical sclerotized hook (Fig. 28.7b); elytron without subapical spine (Fig. 28.8b); ventral surface densely punctate (Fig. 28.9b) 6

4(3) Metacoxal lines parallel (Fig. 28.10a); interlaminary bridge broadly visible (Fig. 28.10a); antennomeres 5–10 flattened dorsoventrally, semicircular in cross section, especially in males (Fig. 28.11a); eastern Palearctic (Map 28.1). . . . . *Amurodytes*, 165

4' Metacoxal lines anteriorly divergent (Fig. 28.10b); interlaminary bridge not broadly visible (Fig. 28.10b); antennomeres not flattened, approximately circular in cross section (Fig. 28.11b) 5

5(4) Body with ventral surface shiny with sparse, coarse punctation (Fig. 28.12a); elytron without subapical spine (Fig. 28.8b); Palearctic (Map 28.6). . . . . *Scarodytes*, 169

5' Body with ventral surface dull and matte from fine and dense punctation or from microreticulation between coarse punctures (Fig. 28.12b), or elytron with subapical spine (Fig. 28.8a); Holarctic south into Africa (Map 28.4) . . . . . *Nebrioporus*, 167

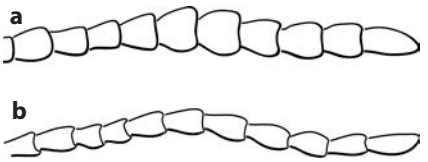


Fig. 28.11. Deronectina right antennae. **a**, *Amurodytes belovi*. **b**, *Scarodytes halensis*.

6(3) Metatibia with anterior surface extensively punctate (Fig. 28.13a); Europe, North America . . . . *Stictotarsus* (in part) *duodecimpustulatus* group, 169

6' Metatibia with anterior surface not punctate (Fig. 28.13b) 7

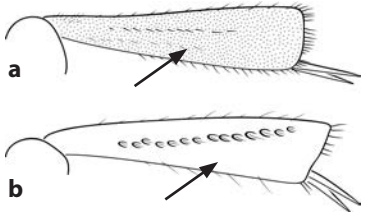


Fig. 28.13. *Stictotarsus* metatibiae. **a**, *S. duodecimpustulatus*. **b**, *S. roffii*.

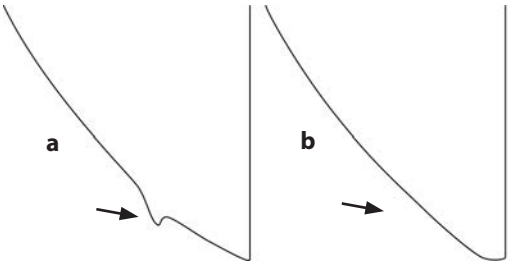


Fig. 28.8. Deronectina left elytral apex. **a**, *Nebrioporus macronychus*. **b**, *Scarodytes halensis*.

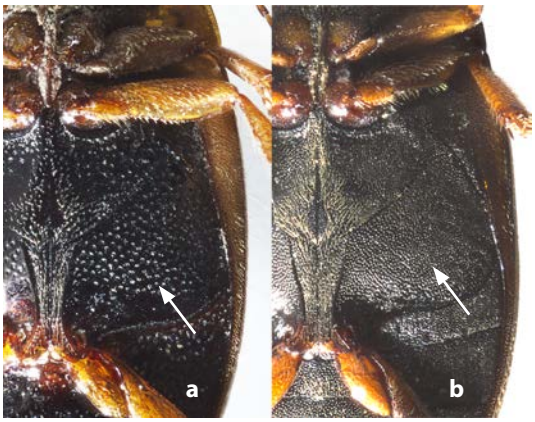


Fig. 28.9. Deronectina ventral surfaces. **a**, *Scarodytes halensis*. **b**, *Boreonectes striatellus*.

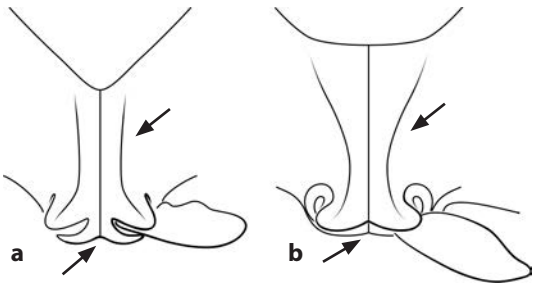


Fig. 28.10. Deronectina metacoxal lines. **a**, *Amurodytes belovi*. **b**, *Nebrioporus canariensis*.

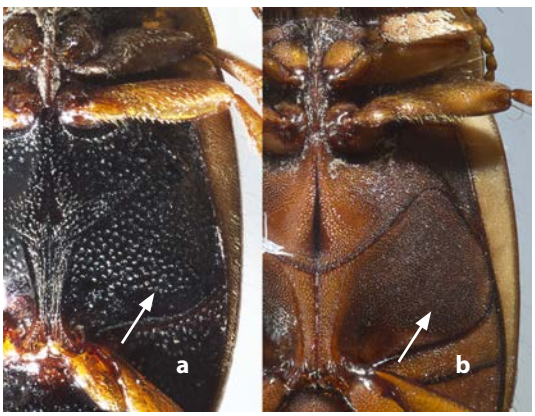


Fig. 28.12. Deronectina ventral surfaces. **a**, *Scarodytes halensis*. **b**, *Nebrioporus assimilis*.

7(6) Prosternal process with apical portion broad and deflexed (Fig. 28.14a); lateral portion of metacoxa rugulose (Fig. 28.15a); North America . . . . *Stictotarsus* (in part) *roffii* group, 169

7' Prosternal process with apical portion not broad and deflexed (Fig. 28.14b); lateral portion of metacoxa not rugulose (Fig. 28.15b) . 8

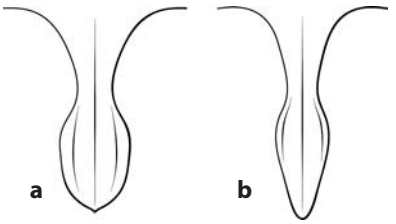


Fig. 28.14. Deronectina prosternal processes. **a**, *Stictotarsus roffii*. **b**, *Boreonectes striatellus*.

8(7) Head transverse (Fig. 28.16a); Holarctic (Map 28.2). . . . . *Boreonectes*, 166

8' Head subquadrangular, elongate (Fig. 28.16b); northwestern Africa and southern Iberia (Map 28.8). . . . . *Trichonectes*, 170

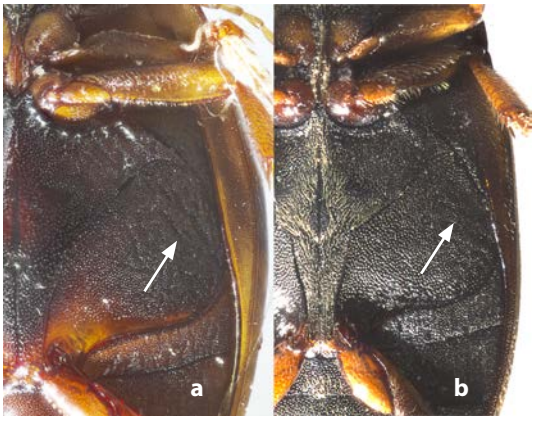


Fig. 28.15. Deronectina ventral surfaces. **a**, *Stictotarsus roffii*. **b**, *Boreonectes striatellus*.

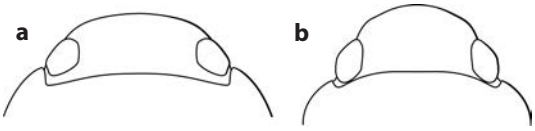


Fig. 28.16. Deronectina heads. **a**, *Boreonectes aequinoctialis*. **b**, *Trichonectes otini*.

Fig. 28.17. *Amurodytes belovi*. Scale = 1.0mm. Reprinted from Fery and Petrov (2013) with permission from Linzer Biologische Beiträge.

Genus *Amurodytes* Fery and Petrov, 2013

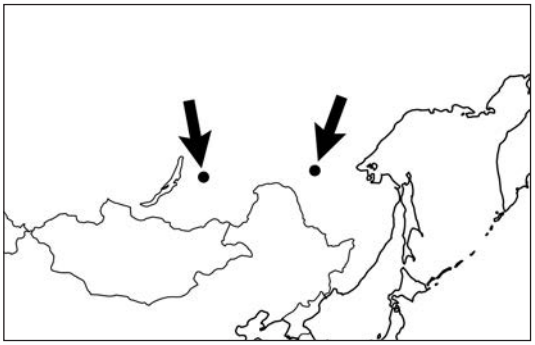
Body Length. 3.4–3.7mm.

Diagnosis. This genus is characterized in Deronectina by: (1) no distinctive longitudinal impressions laterally on the pronotum (Fig. 28.17); (2) the metacoxal processes with the interlaminary bridge exposed (Fig. 28.10a); (3) the metatibia with the anterior surface not covered with punctures; (4) metatarsomere V about 1.5 × the length of IV; and (5) the male lateral lobe without an apical, sclerotized hook. In addition, the dorsal surface in *Amurodytes* is longitudinally vittate (Fig. 28.17), the metacoxal lines are subparallel (Fig. 28.10a), the medial antennomeres are dorsoventrally compressed (Fig. 28.11a), and the protarsomeres do not have ventral adhesive discs. Specimens are fairly robust (Fig. 28.17).

Classification. This genus was recently erected for an unusual species from the eastern Palearctic (Fery and Petrov, 2013). Fery and Petrov (2013) present a narrative examination of the *Deronectes* group of genera and suggest *Amurodytes* may be sister to the group except *Oreodytes*.

Diversity. There is a single species in the genus, *A. belovi* Fery and Petrov.

Natural History. Specimens of *A. belovi* are brachypterus and certainly flightless, but little else is known



Map 28.1. Distribution of *Amurodytes*.

of their biology from the few specimens collected (Fery and Petrov, 2013). Fery and Petrov (2013) suspected that the specimens were collected from fast rivers.

Distribution. The single species is known from two localities in eastern Russia (Map 28.1).

Genus *Boreonectes* Angus, 2010

Body Length. 3.3–6.4mm.

Diagnosis. This genus is characterized in Deronectina by: (1) the pronotum without distinct longitudinal impressions on each side (Fig. 28.18); (2) the metacoxal processes with the interlaminary bridge concealed (as in Fig. 28.5b); (3) the metatibia with the anterior surface not punctate (as in Fig. 28.6b); (4) metatarsomere V about 1.5 × the length of tarsomere IV (as in Fig. 28.5b); (5) the male lateral lobe apically without a sclerotized hook (Fig. 28.7b); (6) the elytron without a subapical spine (Fig. 28.18); (7) the ventral surface densely punctate (Fig. 28.9b); (8) the prosternal process with the apical portion not broad and deflexed (Fig. 28.14b); (9) the meso- and metaventrite not in contact; (10) the lateral portion of the metacoxa not rugulose (Fig. 28.15b); and (11) the dorsal surface glabrous (Fig. 28.18).

Classification. This genus was erected (Angus, 2010a) to include the *Stictotarsus griseostriatus* group of species of Nilsson and Angus (1992). It is difficult to diagnose, and Nilsson and Angus (1992) were unable to identify any specific synapomorphies. The group was paraphyletic with respect to the *Stictotarsus roffii* group based on molecular data (Ribera, 2003). Much of the justification for removing this species group from *Stictotarsus* was based on karyotypic features, including the XX/XO sex determination system (species remaining in *Stictotarsus* have XX/XY sex determination) (Dutton and Angus, 2007; Angus, 2008; 2010a; b; Angus and Tatton, 2011). Angus (2010a) was uncertain whether all the species in the *S. griseostriatus* group would eventually prove to belong to *Boreonectes*, so it is possible the taxon content of the group will change as the group becomes better known.

Fig. 28.18. *Boreonectes aequinoctialis*. Scale = 1.0mm.

Diversity. *Boreonectes* currently includes 16 species. Most of the taxa were revised by Zimmerman and Smith (1975a) and Zimmerman (1982).

Natural History. Members of *Boreonectes* are often extremely abundant inhabitants of temporary pools, slow areas of rivers, and other areas of clear water with mineral substrates. Some occur in saline or alkaline habitats (Zimmerman and Smith, 1975a; Zimmerman, 1982) and coastal rock pools (Nilsson and Holmen, 1995). Karyotypic information for the group has been heavily investigated by Angus (2008; 2010a; b) and Dutton and Angus (2007).

Distribution. This is a primarily Holarctic boreoalpine group with representatives from extreme northern localities south to northern Africa and south into highland areas of Central America (Map 28.2).

Map 28.2. Distribution of *Boreonectes*.

Genus *Deronectes* Sharp, 1882

Body Length. 3.5–6.0mm.

Diagnosis. Among Deronectina, *Deronectes* is characterized by: (1) no longitudinal impressions laterally on the pronotum (Fig. 28.19); (2) metacoxal processes with the interlaminary bridge exposed (Fig. 28.5a); (3) the metatibia with the anterior surface covered with punctures (Fig. 28.6a); (4) meta-

Fig. 28.19. *Deronectes moestus*. Scale = 1.0mm.

tarsomere V about 2 × the length of IV (Fig. 28.5a); and (5) the male lateral lobe without an apical, sclerotized hook. The dorsal surface in *Deronectes* is uniformly black to reddish brown or sometimes bicolored with the anterior part of elytra lighter (Fig. 28.19), whereas the other members of Deronectina are usually fasciate or maculate.

Classification. This genus dates to Sharp's (1882) extraction of several species from *Hydroporus*, though it included species now placed in *Stictotarsus* and *Nebrioporus*. Nilsson and Angus (1992) reinforced the current concept of the genus. Both Ribera *et al.,* (2008), and Miller and Bergsten (2014a) found *Deronectes* to be sister to all other Deronectina. The relationships between *Deronectes* species were studied by Ribera (2003) and Abellan and Ribera (2011).

Diversity. There are 58 species currently assigned to this genus, making it one of the larger genera in the subtribe. Many of them were revised by Fery and Brancucci (1997) and Fery and Hosseinie (1998).

Natural History. *Deronectes* occur especially in small, fast streams and rivers with mineral substrates in mountainous regions, including at high elevation (Fery and Brancucci, 1997). Larvae have been described in a modern context by Alarie *et al.* (1999). They have been used in numerous ecological, physiological, and biogeographic studies (e.g., Sisula, 1971; Pajunen, 1981; Madsen, 2007; 2009; Kehl and Dettner, 2009; Kuechler *et al.*, 2009; Calosi *et al.*, 2010; Sánchez-Fernández *et al.*, 2012).

Distribution. This Palearctic group has members from northwestern Africa north through Europe to Scandinavia and east to western China (Map 28.3).

Map 28.3. Distribution of *Deronectes*.

Genus *Nebrioporus* Régimbart, 1906

Body Length. 3.6–7.8mm.

Diagnosis. This genus is characterized in Deronectina by: (1) the pronotum without distinct longitudinal impressions on each side (Figs. 28.3b,20); (2) the metacoxal processes with the interlaminary bridge concealed (Fig. 28.5b); (3) metatarsomere V about 1.5 × length of tarsomere IV (Fig. 28.5b); (4) the male lateral lobe apically with a sclerotized hook (Fig. 28.7a); (5) the elytron with (Fig. 28.8a) or without (as in Fig. 28.8b) a subapical spine; and (6) the ventral surface densely punctate or microreticulate (Fig. 28.12b).

Classification. Historically, most of the species were placed (also with members of other genera) in the genus *Potamonectes* Zimmermann, but Nilsson and Angus (1992) revised generic concepts and stabilized the classification of this large complex, and *Potamonectes* was synonymized with *Nebrioporus*. Historically, two subgenera were also recognized in the group, but *N.* (*Zimmermannius*) was also synonymized with *Nebrioporus* (Toledo, 2009).

Fig. 28.20. *Nebrioporus macronychus*. Scale = 1.0mm.

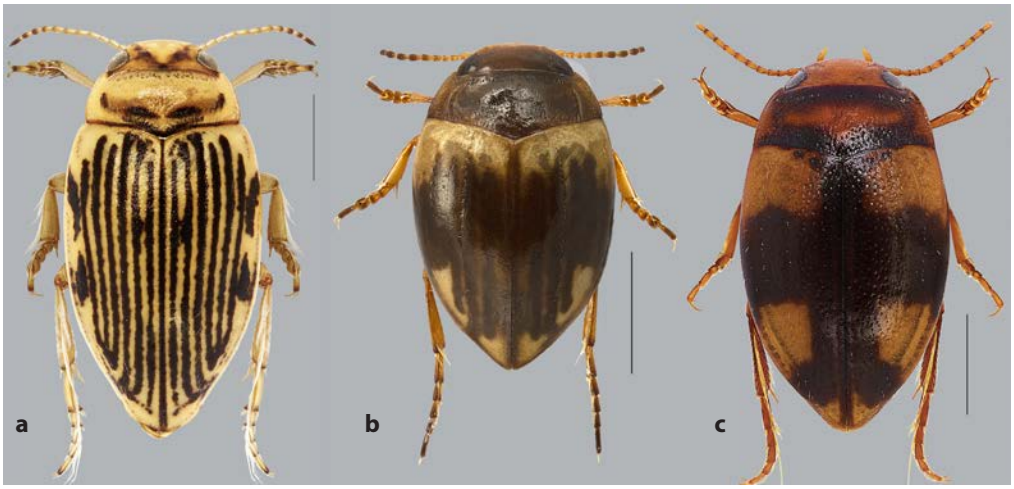


Fig. 28.21. *Oreodytes* species. **a**, *O. alpinus*. **b**, *O. congruus*. **c**, *O. quadrimaculatus*. Scale = 1.0mm.

Diversity. There are currently 58 species in this large, diverse genus, making it as large as *Deronectes* and these two the largest in Deronectina. The group has been revised in combination by Toledo (2009), Nilsson (1992c), and Angus *et al.* (1992).

Natural History. This is a diverse group with members occurring in many habitats from sea level to high elevation mainly in seeps, springs, and streams, though there are representatives in lakes and ditches and even saline habitats (Toledo, 2009). Various aspects of the salinity tolerance of the two halophilic species *N. ceresyi* (Aubé) and *N. baeticus* (Schaum) have been extensively studied (Sánchez-Fernández *et al.*, 2010; Pallarés *et al.*, 2012; 2015; Céspedes *et al.*, 2013).

Distribution. This is a very broadly distributed group with a few members in North America but most of the diversity spread throughout the Palearctic region with a few extending south through the mountains of Africa south to the Cape (Map 28.4).

Map 28.4. Distribution of *Nebrioporus*.

Genus *Oreodytes* Seidlitz, 1887

Body Length. 2.4–5.7mm.

Diagnosis. Within Deronectina, this group is characterized by (1) distinctive longitudinal impressions on the lateral surface of the pronotum (Fig. 28.3a) and (2) pro- and mesotarsomeres I–III with ventral adhesive setae (Fig. 28.4a). Specimens range from globular to elongate, and most are dorsally fasciate to maculate (Fig. 28.21).

Classification. Not all authors have included *Oreodytes* in the *Deronectes* group of genera (e.g., Nilsson and Angus, 1992) but have regarded the genus as the probable sister group of the group. Recent analyses have actually found *Oreodytes* paraphyletic with respect to other members of the *Deronectes* group (e.g., Ribera *et al.*, 2008; Miller and Bergsten, 2014a), suggesting the need for additional cladistic analysis to sort out relationships among these taxa.

Diversity. There are currently 30 species in *Oreodytes*. The North American taxa were treated by Zimmerman (1985), Larson (1990b), Alarie (1993), and Larson *et al.* (2000). Some Palearctic taxa can

Map 28.5. Distribution of *Oreodytes*.

be identified using Zaitzev (1953) and Nilsson and Holmen (1995).

Natural History. *Oreodytes* are lotic, occurring especially in mountain streams and rivers. Several aspects of their biology and ecology were discussed by Larson (1985) and Zack (1992). Larvae have been described by de Marzo (1977), Nilsson (1987c), Alarie *et al.* (1996), and Alarie (1997).

Distribution. This is a Holarctic group in northern and central North America, Europe, and north Asia to the Russian far east and Japan (Map 28.5).

Genus *Scarodytes* Gozis, 1914

Body Length. 3.7–5.2mm.

Diagnosis. *Scarodytes* are characterized in Deronectina by: (1) the pronotum without distinct longitudinal impressions on each side (Fig. 28.22); (2) the metacoxal processes with the interlaminary bridge concealed; (3) metatarsomere V about 1.5 × length of tarsomere IV; (4) the male lateral lobe apically with a sclerotized hook; (5) the elytron without a subapical spine (Fig. 28.22); and (6) the ventral surface shiny and sparsely punctate (Fig. 28.12a).

Classification. *Scarodytes* was originally described as a subgenus of *Hydroporus* (des Gozis, 1910-1914) but given generic rank by Falkenström (1939). The genus is similar in many respects to *Nebrioporus* (Nilsson and Angus, 1992) but was found most closely related to the *Stictotarsus duodecimpustulatus* species group (Ribera, 2003; Ribera *et al.*, 2008)

Diversity. There are currently 10 species. They were treated in large part by Fery and Stastny (2007).

Fig. 28.22. *Scarodytes halensis*. Scale = 1.0mm.

Natural History. Specimens have been usually collected from streams with mineral substrates. Larvae were described by Alarie *et al.* (1999).

Distribution. This is a western Palearctic genus with members from northern Africa across Europe to the eastern Mediterranean region (Map 28.6).

Map 28.6. Distribution of *Scarodytes*.

Genus *Stictotarsus* Zimmermann, 1919

Body Length. 3.8–6.3mm.

Diagnosis. This genus is characterized in Deronectina by: (1) the pronotum without distinct longitudinal impressions on each side (Fig. 28.23); (2) the metacoxal processes with the interlaminary bridge concealed or not; (3) the metatibia with the anterior surface punctate (Fig. 28.13a) or not (Fig. 28.13b); (4) metatarsomere V about 1.5 × the length of tarsomere IV; (5) the male lateral lobe apically without a sclerotized hook; (6) the elytron without a subapical spine (Fig. 28.23); (7) the ventral surface densely punctate (28.15a); (8) the prosternal process with the apical portion broad and deflexed (Fig. 28.14a) or not; (9) the meso- and metaventrite in contact; and (10) the lateral portion of the metacoxa rugulose (Fig. 28.15a) or not.

Classification. This genus is currently in a state of taxonomic change. Nilsson and Angus (1992) recognized three groups in their revised concept of *Stictotarsus*, and one of these, the *S. griseostriatus* group, was placed in a new genus, *Boreonectes* by Angus (2010b). The other two groups associated with the genus are the *S. roffii* group, with members in western and southwestern North America, and the *S. duodecimpustulatus* group, with species in Europe and North America. There is molecular evidence that these two groups are not closely related (Ribera, 2003; Ribera *et al.*, 2008), and the taxonomy of this

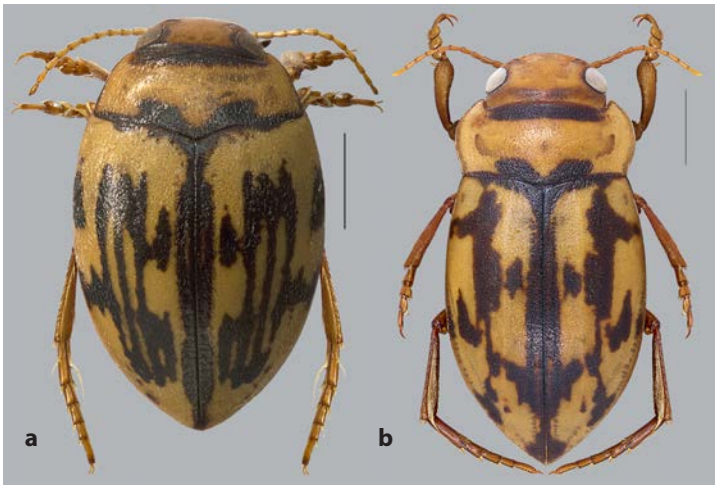


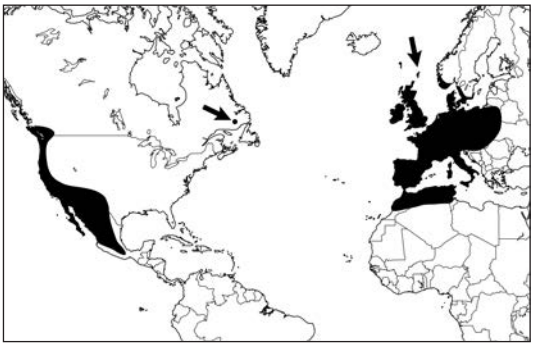
Fig. 28.23. *Stictotarsus* species. **a**, *S. falli*. **b**, *S. duodecimpustulatus*. Scale = 1.0mm.

genus will probably change. The *Stictotarsus roffi* group seems to be closely related to *Boreonectes* whereas the *S. duodecimpustulatus* group is sister to *Scarodytes*.

Diversity. With both groups, the genus includes 18 species. The North American species were revised by Zimmerman and Smith (1975a) and Zimmerman (1982) with another species added later by Larson (1991a).

Natural History. These species live especially in streams or rock pools with mineral substrates.

Distribution. Species now assigned to *Stictotarsus* occur in southwestern North America, eastern Canada, and throughout much of Europe (Map 28.7).



Map 28.7. Distribution of *Stictotarsus*.

Genus *Trichonectes* Guignot, 1941

Body Length. 4.7–5.4mm.

Diagnosis. This genus is characterized in Deronectina by: (1) the pronotum without distinct longitudinal impressions on each side (Fig. 28.24); (2) the metacoxal processes with the interlaminary bridge concealed; (3) the metatibia with the anterior surface not punctate; (4) metatarsomere V about 1.5 × length of tarsomere IV; (5) the male lateral lobe apically without a sclerotized hook; (6) the elytron without a subapical spine (Fig. 28.24); (7) the ventral surface densely punctate; (8) the prosternal process with the apical portion not broad and deflexed; (9) the meso- and metaventrite not in contact; (10) the lateral portion of the metacoxa not rugulose; and (11) the dorsal surface densely setose (Fig. 28.24). The head is subquadrate, and specimens are longitudinally striped (Fig. 28.24).

Classification. The genus name was erected as a subgenus of *Potamonectes* Zimmermann. It was later placed in synonymy with *Stictotarsus* (Nilsson and Angus, 1992) until resurrected by Ribera

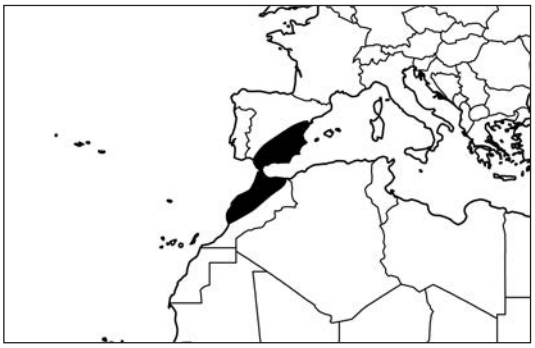
Fig. 28.24. *Trichonectes otini*. Scale = 1.0mm.

(2003). *Trichonectes otini* was found as sister to a group consisting of *Nebrioporus*, *Scarodytes* and the *Stictotarsus duodecimpustulatus* species group by Ribera (2003) and Ribera *et al*. (2008).

Diversity. The only species in the genus is *Trichonectes otini* Guignot.

Natural History. According to Millán *et al*. (2014), *Trichonectes* occupies salt creeks and streams in arid regions of inland southern Spain.

Distribution. *Trichonectes otini* is found along the southern edge of the Iberian Penninsula and northwestern Africa (Map 28.8).



Map 28.8. Distribution of *Trichonectes*.

29. Subtribe Siettitiina

Body Length. 1.6–4.0mm.

Diagnosis. This is a difficult group to diagnose. Siettitiina has one potential synapomorphy — the female genitalia has a ring-shaped sclerite on the bursa, possibly homologous with the receptacle in other Hydroporinae (Fig. 29.1, Miller, 2001c; Miller *et al.*, 2006; 2009b) — though not all taxa have been surveyed for this feature. Also, this structure is not convincingly evident in *Graptodytes*, but plenty of other evidence suggests they are part of this group (see below). *Stictonectes*, *Siettitia*, *Etruscodytes*, *Graptodytes*, and *Rhithrodytes* have a distinct longitudinal groove along each side of the pronotal disc (as in Fig. 29.2b,c), but other genera do not. The group also includes several subterranean genera that have the modifications characteristic of these taxa, including depigmentation, microphthalmy, flightlessness, etc. (e.g., Fig. 29.7).

Classification. This family group was originally conceived to include several subterranean Hydroporinae (Smrž, 1982) which do not appear to be closely related, though the group does include a number of stygobionts. Other investigators noted similarities between certain subterranean Palearctic species and the epigean *Graptodytes* and related genera (Abeille de Perrin, 1904; Castro and Delgado, 2001). Ribera *et al.* (2002b; 2008), Ribera and Faille (2010), Miller *et al.* (2013), and Miller and Bergsten (2014a) found these genera to be monophyletic, and Miller and Bergsten (2014a) formally recognized the group as a subtribe of Hydroporini.

Diversity. There are 11 genera in the subtribe, including the recently transferred *Stygoporus*.

Natural History. Most members of this group are characteristic of seeps, springs, and streams. Several members of the group are found in underground waters, including the species found in North America (Miller *et al.*, 2009b).

Distribution. Most species occur in areas around the Mediterranean with three known subterranean genera in North America.

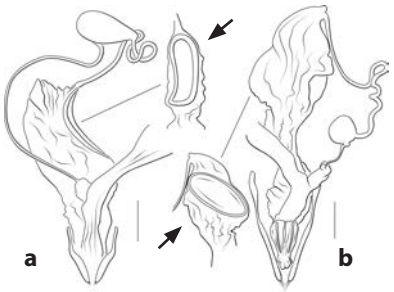


Fig. 29.1. Siettitiina female reproductive tract, ventral aspect and ring-shaped sclerite. **a**, *Ereboporus naturaconservatus*. **b**, *Stictonectes epipleuricus*. Scale = 0.1mm.

Key to the Epigean Genera of Siettitiina

Several taxa in Siettitiina — including *Ereboporus*, *Psychopomporus*, *Etruscodytes*, *Siettitia*, *Iberoporus*, *Stygoporus*, and at least one species of *Graptodytes* — are subterranean. These have features common to subterranean diving beetles (see Fig. 3.51, flightless, eyeless, depigmented) and are keyed separately in the key to subterranean taxa (page 45).

1 Pronotum with longitudinal impressed line on each side (Fig. 29.2b,c). 2
1' Pronotum without longitudinal impressed line on each side (Fig. 29.2a) 4

2(1) Ventral surface shagreened (Fig. 29.3a); western Palearctic (Map 29.10) . . *Stictonectes*, 178
2' Ventral surface reticulate (Fig. 29.3b) 3

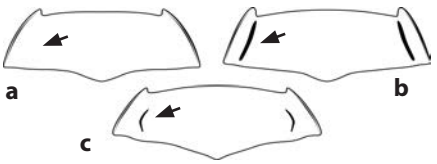


Fig. 29.2. Siettitiina pronota. **a**, *Metaporus meridionalis*. **b**, *Rhithrodytes sexguttatus*. **c**, *Graptodytes ignotus*.

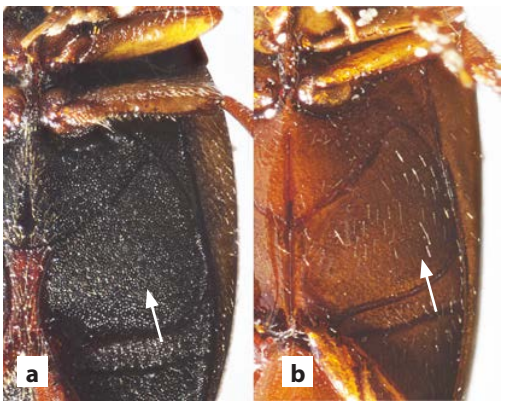


Fig. 29.3. Siettitiina ventral surfaces. **a**, *Stictonectes optatus*. **b**, *Rhithrodytes sexguttatus*.

3(2) Pronotal line on each side extending nearly entire length of pronotum (Fig. 29.2b); apex of median lobe hooked (Fig. 29.4a); southern Europe (Map 29.8). . . . . *Rhithrodytes*, 177

3' Pronotal line on each side short, not extending entire length of pronotum (Fig. 29.2c); apex of median lobe not hooked (Fig. 29.4b); western Palearctic (Map 29.3) . . . . . *Graptodytes*, 174

4(1) Dorsal surface alutaceous (Fig. 29.5a); size larger (>2.9mm); western Palearctic (Map 29.6). . . . . *Porhydrus*, 176

4' Dorsal surface distinctly reticulate (Fig. 29.5b); size smaller (<2.9mm); western Palearctic and Middle East (Map 29.5) . . . . .*Metaporus*, 175

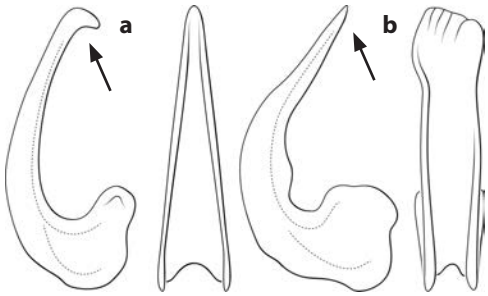


Fig. 29.4. Siettitiina male genitalia, median lobe right lateral aspect, median lobe ventral aspect. **a**, *Graptodytes granularis.* **b**, *Rhithrodytes crux.*

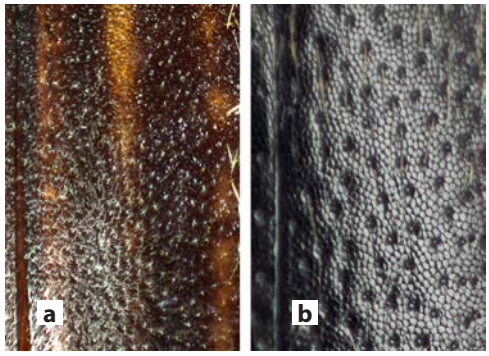


Fig. 29.5. Siettitiina elytral surface. **a**, *Porhydrus lineatus*. **b**, *Graptodytes ignotus.*

Genus *Ereboporus* Miller, Gibson, and Alarie, 2009

Body Length. 2.3–2.4mm.

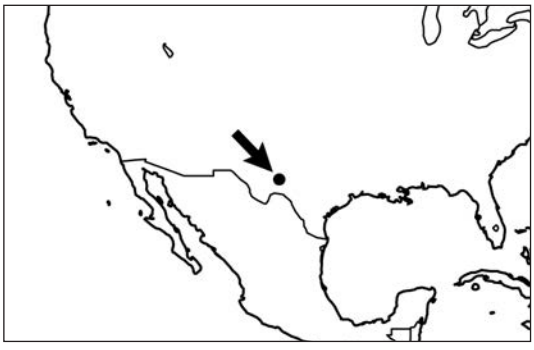
Diagnosis. *Ereboporus* are subterranean and have the eyes absent, flight wings reduced and elytra fused, reduced pigmentation, and other features typical of subterranean species (Fig. 29.6). *Ereboporus* are unique in having an extremely large head and a small pronotum that is cordate (Fig. 29.6). The elytra curve around ventrally, covering large areas of the surfaces of the abdominal sternites (Fig. 3.44a).

Classification. The species in this genus is one of only three members of the subtribe (Miller and Bergsten, 2014a) found in North America (the others are *Psychopomporus felipi* and *Stygoporus oregonensis*), all of which are subterranean (Miller *et al.*, 2009b; Jean *et al.*, 2012).

Diversity. There is a single species in this genus, *E. naturaconservatus* Miller, Gibson and Alarie.

Natural History. The few specimens of the single

Fig. 29.6. *Ereboporus naturaconservatus.* Scale = 1.0mm.



Map 29.1. Distribution of *Ereboporus*.

species were collected having washed out of a large spring originating in the Edwards-Trinity Aquifer of central Texas, USA, a large karst aquifer (Miller *et al.*, 2009b). Larvae were described by Alarie *et al.* (2013).

Distribution. *Ereboporus* are only known from Caroline Springs, Independence Creek, Terrell County, Texas, USA (Map 29.1).

Genus *Etruscodytes* Mazza, Cianferoni, and Rocchi, 2013

Body Length. 2.3–2.5mm.

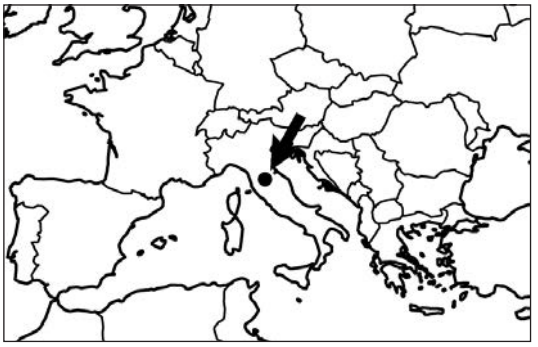
Diagnosis. This genus is subterranean and exhibits the characteristics typical of diving beetles in that habitat, including depigmentation, flightlessness, microphthalmy, etc. (Fig. 29.7). The genus differs from other subterranean members of the subtribe, except *Siettitia* and *Stygoporus*, in having distinctive longitudinal striae on the lateral surfaces of the pronotum (Fig. 29.7). From these two genera the genus differs in the broad, laterally subangulate head (see Figs. 3.47a,29.7, evenly rounded in *Siettitia* and *Stygoporus*, as in Fig. 3.47b), and the prosternal process apically reaching the metaventrite (narrowly separated from the metaventrite in *Siettitia*).

Classification. Mazza *et al.* (2013) discussed *Etruscodytes* relationships to other Siettitiina, and it is likely related to *Siettitia* and *Iberoporus*.

Diversity. There is a single species in this genus, *E. nethuns* Mazza, Cianferoni, and Rocchi.

Natural History. The type series of the single *Etruscodytes* species was collected by pumping water from a well. Specimens of *Niphargus* Schiödte (Amphipoda) were also collected.

Distribution. The species is known only from a site near Florence, Tuscany, Italy (Map 29.2).



Map 29.2. Distribution of *Etruscodytes*.

Genus *Graptodytes* Seidlitz, 1887

Body Length. 1.6–4.0mm.

Diagnosis. This genus is very similar to *Rhithrodytes* in having a thin, distinctive impressed line on the lateral surface of the pronotum (Fig. 29.8) and the dorsal and ventral surfaces shiny and variously microreticulate. *Graptodytes* differs from *Rhithrodytes* in having the impressed lines on the pronotum short (Figs. 29.2c,8), whereas in *Rhithrodytes* the lines extend nearly the entire length of the pronotum (Figs. 29.2b,13). Species are also similar to *Metaporus*, but that genus lacks pronotal lines (Fig. 29.10). One species, the subterranean *G. eremitus* Ribera and Faille,

Fig. 29.7. *Etruscodytes nethuns.* Scale = 1.0mm.

Fig. 29.8. *Graptodytes ignotus.* Scale = 1.0mm.

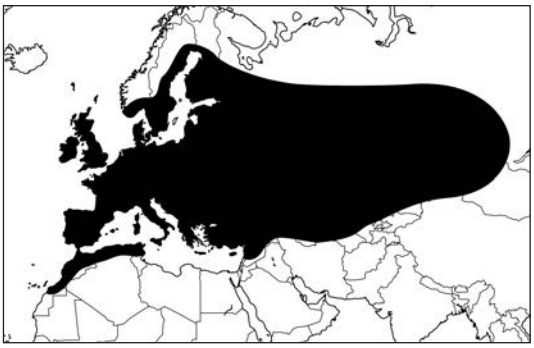
also lacks the impressed lines typical of *Graptodytes*, but the male genitalia and body shape (as well as molecular data) place the species within that genus (Ribera and Faille, 2010). Many specimens are shiny and attractively marked with maculae or fasciae (Fig. 29.8).

Classification. This genus historically included many species in other genera currently in the subtribe (Seidlitz, 1887). Ribera and Faille (2010) thought *Graptodytes* is related to *Metaporus* and *Siettitia*.

Diversity. There are currently 22 species in the genus. There is no modern comprehensive revision, but many species can be identified using Zimmermann (1932), Zaitzev (1953), Franciscolo (1979a), Nilsson and Homen (1995).

Natural History. Most members of *Graptodytes* occur in a variety of small water bodies, especially lentic habitats. Several species, however, are found in interstitial or rheophilic areas of small seeps or springs, with at least one distinctly subterranean species (Ribera and Faille, 2010).

Distribution. *Graptodytes* are found from north Africa through Europe east to east Siberia (Map 29.3).



Map 29.3. Distribution of *Graptodytes*.

Genus *Iberoporus* Castro and Delgado, 2001

Body Length. 2.0–2.2mm.

Diagnosis. *Iberoporus* are subterrranean, microphthalmic, flightless, and depigmented (Fig. 29.9). They differ from other subterranean siettitiines by: (1) absence of longitudinal lines on the sides of the pronotum (Fig. 29.9); (2) absence of an elongate, tuberculate projection near the base of the prosternal process (though *Iberoporus* have a toothlike process); (3) the elytra not extending ventrally over the abdomen; and (4) the pronotum distinctly cordate and widest anterior of the middle (Fig. 29.9).

Fig. 29.9. *Iberoporus cermenius*. Scale = 1.0mm.

Classification. Relationships of *Iberoporus* are not well known, though Castro and Delgado (2001) thought they are related to *Siettitia* and *Rhithrodytes*.

Diversity. There is a single species in the genus, *I. cermenius* Castro and Delgado.

Natural History. The single species is subterranean. It is negatively bouyant and sinks rather than floats, apparently because it does not carry air under the elytra when submerged (Castro and Delgado, 2001). It feeds in captivity on chironomid larvae (Castro and Delgado, 2001).

Distribution. The species is known only from a well in Priego de Córdoba, southern Spain (Map 29.4).

Map 29.4. Distribution of *Iberoporus*.

Genus *Metaporus* Guignot, 1945

Body Length. 2.2–2.8mm.

Diagnosis. This genus is very similar to *Graptodytes* and *Rhithrodytes* in having the dorsal and ventral

Fig. 29.10. *Metaporus meridionalis*. Scale = 1.0mm.

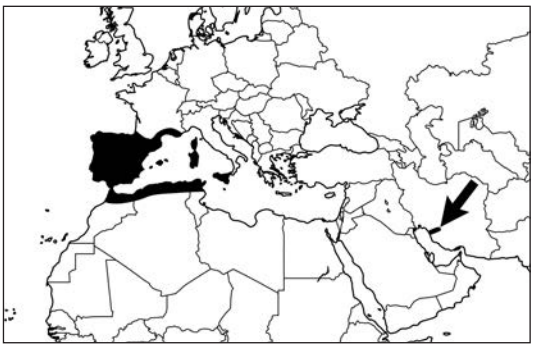
surfaces shiny and variously microreticulate (as in Fig. 29.5b), but *Metaporus* lack impressed lines laterally on the pronotum (Figs. 29.2a,10).

Classification. The genus is likely closely related to *Graptodytes* (Ribera and Faille, 2010).

Diversity. There are two species currently recognized in the genus, *M. meridionalis* (Aubé) and *M. orientalis* Toledo and Hosseinie. Each of these were diagnosed by Toledo and Hosseinie (2003).

Natural History. *Metaporus* occur in streams, marshes, and ponds. They are also rheophilic and found deep in streamside gravel (Ribera and Faille, 2010).

Distribution. *Metaporus* have a disjunct distribution with *M. meridionalis* in western Europe and northern Africa and *M. orientalis* in Iran (Map 29.5).



Map 29.5. Distribution of *Metaporus*.

Genus *Porhydrus* Guignot, 1945

Body Length. 3.0–3.5mm.

Fig. 29.11. *Porhydrus obliquesignatus*. Scale = 1.0mm.

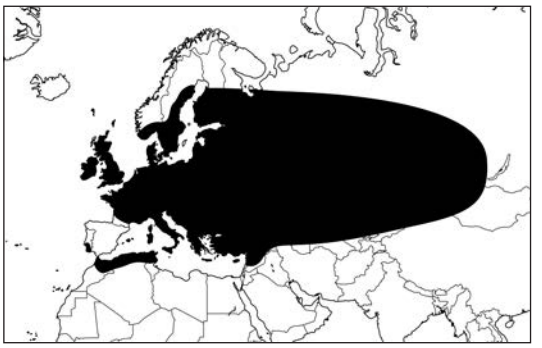
Diagnosis. *Porhydrus* are small, lack an impressed line on each side of the pronotum (Fig. 29.11), and have the dorsal surface finely punctate and alutaceous, not shiny and reticulate (Fig. 29.5a).

Classification. There is no clear evidence of *Porhydrus* relationships with other Siettitiina.

Diversity. The four species in *Porhydrus* were treated by Franciscolo (1979a) and Guignot (1959b).

Natural History. Specimens can be found in a variety of habitats, including small ponds, ditches, and slow streams. Larvae were described by Meinert (1901).

Distribution. This is a Palearctic group with members throughout much of Europe south to northern Africa and east to Siberia (Map 29.6).



Map 29.6 Distribution of *Porhydrus*.

Genus *Psychopomporus* Jean, Telles, and Miller 2012

Body Length. 2.0mm.

Fig. 29.12. *Psychopomporus felipi.* Scale = 1.0mm.

Diagnosis. *Psychopomporus* are subterranean and have the eyes absent, flight wings reduced and elytra fused, reduced pigmentation, and other features typical of subterranean species (Fig. 29.12). Specimens also have the prosternal process rather strongly declivous, apically extending to the anterior projection of the metaventrite and with a prominent medial projection, the mesotibia expanded and strongly arcuate in males, and the elytral epipleuron broad and flat anteriorly (Jean *et al.,* 2012).

Classification. This is one of three North American members of the subtribe (the others are *Ereboporus naturaconservatus* and *Stygoporus oregonensis*), all stygobiontic.

Diversity. There is a single species in the genus, *P. felipi* Jean, Telles, and Miller.

Natural History. Specimens are subterranean with a few specimens collected having washed out of a spring originating in the Edwards Trinity Aquifer of Texas, USA, a large karst aquifer (Jean *et al.*, 2012).

Distribution. *Psychopomporus* are only known from San Felipe Springs in Del Rio, Val Verde County, Texas, USA (Map 29.7).

Map 29.7. Distribution of *Psychopomporus*.

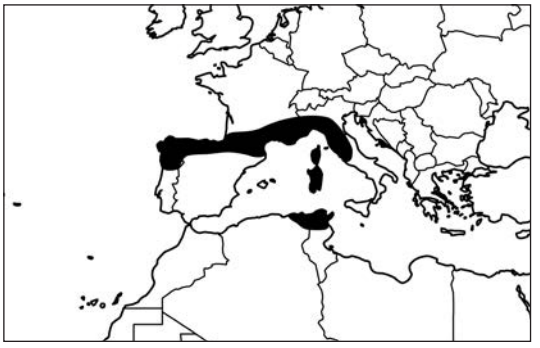
Fig. 29.13. *Rhithrodytes sexguttatus.* Scale = 1.0mm.

Genus *Rhithrodytes* Bameul, 1989

Body Length. 2.3–3.3mm.

Diagnosis. This genus is very similar to *Graptodytes* in having a thin, distinctive impressed line on the lateral surface of the pronotum (Figs. 29.2b,13) and the dorsal and ventral surfaces shiny and variously microreticulate (Fig. 29.3b). *Rhithrodytes* differs from *Graptodytes* in having the impressed lines on the pronotum extending nearly the entire length of the pronotum (Figs. 29.2b,13), whereas in *Graptodytes* the line is short (Figs. 29.2c,8). Many specimens are shiny and attractively marked with maculae (Fig. 29.13).

Classification. This genus was erected for four species previously placed in *Graptodytes* (Bameul, 1989). The group is evidently a part of the *Graptodytes* group of genera probably related to *Graptodytes* and *Siettitia* (Ribera *et al.*, 2008; Ribera and Faille, 2010; Miller and Bergsten, 2014a).



Map 29.8. Distribution of *Rhithrodytes*.

Diversity. There are currently six species in the genus, apart from the original four an additional species was described by Foster (1992), and another has been resurrected from synonymy (Bilton and Fery, 1996). The group was treated mainly by Bameul (1989; 1996) and Bilton and Fery (1996).

Natural History. *Rhithrodytes* are characteristic of seeps and springs, with some species in interstitial habitats (Bameul, 1989; Bilton and Fery, 1996).

Distribution. Members of this group are found in western and southern Europe and northern Africa (Map 29.8).

Genus *Siettitia* Abeille de Perrin, 1904

Body Length. 2.2–2.5mm.

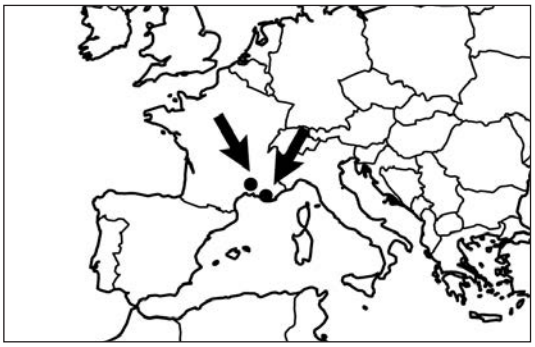
Diagnosis. These are subterranean, flightless, depigmented, and microphthalmic siettitiines (Fig. 29.14). They can be diagnosed from most other subterranean members of the group (except *Stygoporus* and *Etruscodytes*) by the presence of incised lines on each side of the pronotum (Fig. 29.14). *Siettitia* differ in the prosternal process not reaching the metaventrite.

Classification. Little to nothing is known of *Siettitia* relationships, though they have been regarded as possibly closely related to *Rhithrodytes* and *Iberoporus* (Castro and Delgado, 2001; Ribera and Faille, 2010).

Diversity. There are two species in *Siettitia*, *S. avenionensis* Guignot and *S. balsetensis* Abeille de Perrin.

Natural History. *Siettitia* are subterranean and have been collected from wells in southern France.

Distribution. *Siettitia* have been found in Avignon and Le Beausset in southern France (Map 29.9).



Map 29.9. Distribution of *Siettitia*.

Genus *Stictonectes* Brinck, 1943

Body Length. 2.5–3.9mm.

Diagnosis. *Stictonectes* are characterized among the Siettitiina by the ventral surface conspicuously shagreened, or with a distinctive microgranular surface sculpturing (Fig. 29.3a). Like several genera in the group, *Stictonectes* have a pair of impressed, longitudinal pronotal striae (Fig. 29.15). Specimens are robust and often marked dorsally with fasciae or maculae (Fig. 29.15).

Classification. Relationships of the genus to other genera in Siettitiina are not completely clear, but this genus and *Porhydrus* each have stellate punctation, which has been suggested to be a synapomorphy of the two genera (Ribera, 2003; Millán *et al.*, 2013).

Diversity. *Stictonectes* includes 12 similar species,

Fig. 29.14. *Siettitia avenionensis*. Scale = 1.0mm.

Fig. 29.15. *Stictonectes optatus*. Scale = 1.0mm.

some of which were recently described (Bilton, 2012; Millán *et al.*, 2012).

Natural History. Specimens are found in a variety of habitats, but especially on mineral substrates in slow streams and pools in streams or in otherwise dry streambeds. Larvae have been described by Alarie and Nilsson (1997). Millán *et al.* (2012) presented predictive mapping for the Iberian species using environmental niche modeling techniques.

Distribution. *Stictonectes* occur across western Europe north through the British Islands and in areas of northern Africa (Map 29.10).

Map 29.10. Distribution of *Stictonectes*.

Genus *Stygoporus* Larson and LaBonte, 1994

Body Length. 1.8–2.1mm.

Diagnosis. *Stygoporus* are very similar to other stygobitic species in Siettitiina, especially *Etruscodytes* and *Siettitia* species. These three genera have a longitudinal line on each side of the pronotum (Fig. 29.16), also like in several other epigean genera in the tribe. They also generally lack natatory setae on the legs. *Etruscodytes* have a large, rhomboid head, and *Siettitia* have the prosternal process not reaching the metaventrite. *Stygoporus* have a rounded head and prosternal process reaching the metaventrite.

Classification. Although retained in Hydroporina by

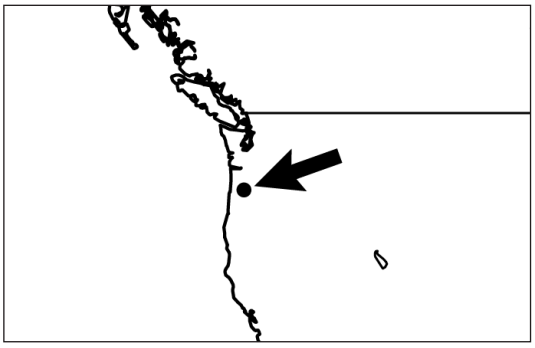
Fig. 29.16. *Stygoporus oregonensis*. Scale = 1.0mm.

Miller and Bergsten (2014a), Kanda *et al.* (in preparation) recently rediscovered the species and determined it to be a North American representative of Siettitiina, like *Ereboporus* and *Psychopomporus*.

Diversity. There is only one species in the genus, *S. oregonensis* Larson and LaBonte.

Natural History. Specimens have been collected from wells in a limited area of western Oregon (Larson and Labonte, 1994; Kanda *et al.,* in preparation). The original well was shock-treated with chlorine (Larson and Labonte, 1994).

Distribution. The species is known only from areas around Dallas, Oregon, USA (Map 29.11).



Map 29.11. Distribution of *Stygoporus*.

30. Subtribe Sternopriscina

Body Length. 1.0–6.5mm.

Diagnosis. This subtribe has few distinguishing features, though all have the elytral epipleuron relatively broad in the apical half narrowing only gradually posteriorly (Fig. 30.1). A few other Hydroporini have the elytral epipleuron relatively broad throughout (e.g., *Deronectes*, Fig. 28.5a), and members of one genus in this clade, *Paroster*, have the epipleuron clearly more narrow apically (Fig. 30.6a). In general, sternopriscines are fairly robust and often attractively marked. Many of them are large for hydroporines, though others are extremely small. This group includes a great many subterranean Australian species that are depigmented, pale, eyeless, and have other morphological adaptations for a subterranean lifestyle (Fig. 30.18b,c).

Classification. These genera have been historically regarded as monophyletic and have been called the *Necterosoma* group of genera (Ribera *et al.*, 2002b; 2008; Balke and Ribera, 2004). Miller and Bergsten (2014a) elevated the informal genus group to a subtribe of Hydroporini. *Carabhydrus* was previously placed in its own tribe, Carabhydrini Watts, based in part on fusion of the metacoxa with abdominal ventrite I, a weakly deflexed prosternum, and a characteristic habitus (Fig. 30.2a, Watts, 1978). Watts *et al.* (2007) later abandoned use of the tribe, placing it in synonymy with Hydroporini. Each of the above features is derived within Sternopriscina, and based on this Carabhydrini was synonymized with Sternopriscina by Miller and Bergsten (2014a).

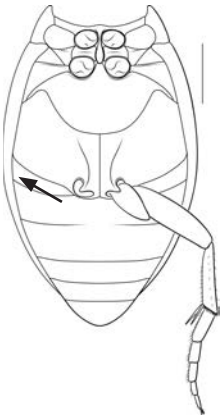


Fig. 30.1. *Chostonectes gigas* ventral surfaces. Scale = 1.0mm.

Diversity. The group currently comprises 11 genera.

Natural History. Sternopriscines occur in an astonishingly broad range of habitats from streams to ponds to rivers. There are a remarkable number of species in two groups, *Paroster* and *Carabhydrus*, that occur in rheophilic and subterranean systems. *Paroster*, in particular, has a rich radiation in west Australian subterranean paleodrainages (Watts *et al.*, 2008; Watts and Humphreys, 2009; Leys *et al.*, 2010). The evolutionary history of the group was studied by Toussaint *et al.* (2015b).

Distribution. Sternopriscina species are all found in Australia north into New Guinea. This is a uniquely Australian radiation within Hydroporinae.

Key to the Epigean Genera of Sternopriscina

There are a large number of subterranean sternopriscine species in *Carabhydrus,* and especially *Paroster*, in Australia. These species are flightless, eyeless, and depigmented (see Fig. 3.51) and are keyed separately in the key to subterranean taxa (page 45).

1 Lateral margins strongly discontinuous between pronotum and elytron, pronotum widest anterior to middle, body elongate (Fig. 30.2a); scutellum exposed with the elytra closed (Fig. 30.2a); elytron each with two longitudinal grooves (Fig. 30.2a); eastern Australia (Map 30.4). . . . . *Carabhydrus*, 184

1′ Lateral margins not strongly discontinuous between pronotum and elytron, pronotum widest near posterior margin, body various (Fig. 30.2b); scutellum concealed (Fig. 30.2b); elytron with four grooves (Fig. 30.12) or without any grooves (Fig. 30.2b) 2

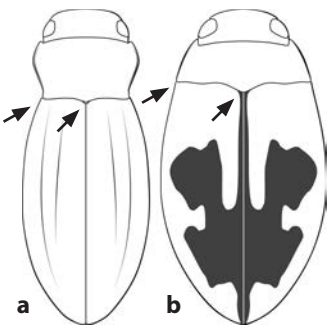


Fig. 30.2. Sternopriscina habitus. **a**, *Carabhydrus niger*. **b**, *Megaporus howittii.*

2(1) Pro- and mesotarsi distinctly pentamerous, tarsomere IV conspicuous and elongate (Fig. 30.8a); male protibia ventrally with small emargination (Fig. 30.3) 3

2′ Pro- and mesotarsi pseudotetramerous (tarsomere IV short, hidden in lobes of III, Fig. 30.8b–d), or actually tetramerous (Fig. 30.8e) or trimerous (Fig. 30.8f); male protibia not ventrally emarginate 4

3(2) Metacoxal process medially produced into V-shaped posterior projection (Fig. 30.4a); metacoxal cavities distinctly separated (Fig. 30.4a); size smaller (total length < 4.5mm); Australia (Map 30.11) . . . . . *Sternopriscus*, 188

3′ Metacoxal process with posterior margin medially with V-shaped emargination (Fig. 30.4b); metacoxal cavities closely approximated (Fig. 30.4b); size larger (total length > 3.3mm); Australia and New Caledonia (Map 30.7). . . . . *Necterosoma*, 186

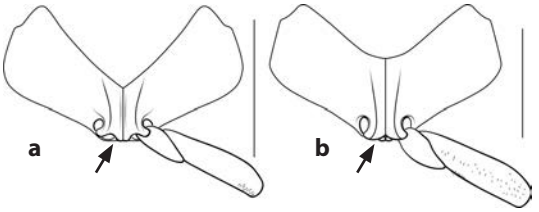


Fig. 30.4. Sternopriscina metacoxae, metalegs. **a**, *Sternopriscus clavatus*. **b**, *Necterosoma penicillatum*. Scales = 1.0mm.

4(2) Anterior surface of metatiba impunctate (Fig. 30.5a,b) 5

4′ Anterior surface of metatibia punctate (Fig. 30.5c). 7

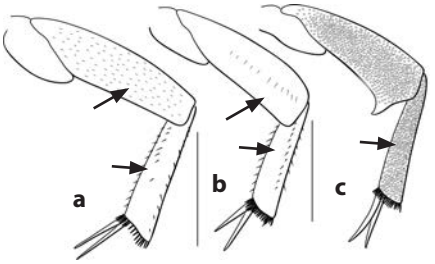


Fig. 30.5. Sternopriscina metalegs. **a**, *Chostonectes gigas*. **b**, *Megaporus howittii*. **c**, *Antiporus gilbertii*. Scales = 1.0mm.

5(4) Elytral epipleuron abruptly narrowed, slender apically, with transverse carina at humeral angle (Fig. 30.6a); size smaller (length <4.2mm); Australia (Map 30.8) . . . . . *Paroster*, 187

5′ Elytral epipleuron gradually narrowed, apically broad, without a transverse carina at humeral angle (Fig. 30.6b); size larger (total length > 3.5mm); 6

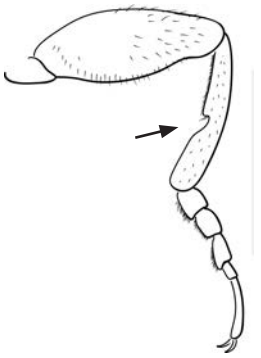


Fig. 30.3. *Necterosoma penicillatum* male proleg. Scale = 1.0mm.

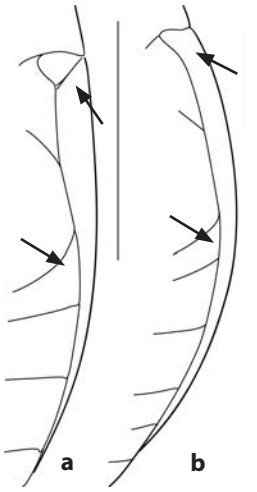


Fig. 30.6. Sternopriscina left ventral surfaces. **a**, *Paroster pallescens*. **b**, *Chostonectes gigas*. Scales = 1.0mm.

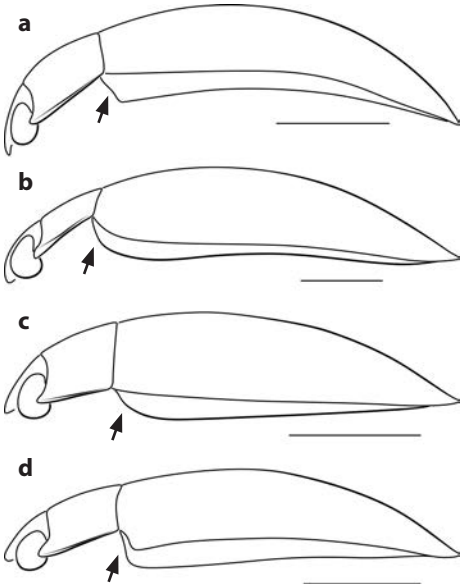


Fig. 30.7. Sternopriscina left lateral aspect. **a**, *Barretthydrus tibialis*. **b**, *Antiporus gilbertii*. **c**, *Sekaliporus kriegi*. **d**, *Tiporus josepheni*. Scales = 1.0mm.

6(5) Metafemur apically slender with anterodorsal angle produced and angulate (Fig. 30.5a); Australia and New Guinea (Map 30.5) . . . . . *Chostonectes*, 185

6′ Metafemur apically robust with anterodorsal angle rounded (Fig. 30.5b); Australia, New Guinea and New Caledonia (Map 30.6) . . . . . *Megaporus*, 185

7(4) Elytron with four longitudinal grooves (Fig. 30.12); male with two protarsal claws (Fig. 30.8c); southeastern Australia (Map 30.2) . . . . . *Barretthydrus*, 183

7′ Elytron without longitudinal grooves; male with a single protarsal claw (Fig. 30.8d–f) . . 8

8(7) Male protarsi with three tarsomeres (Fig. 30.8f); elytral epipleuron sharply bent at humeral angle (Fig. 30.7d); northern Australia (Map 30.12) . . . . . *Tiporus*, 189

8′ Male protarsi with four tarsomeres (Fig. 30.8e); elytral epipleuron nearly continuous with pronotum in straight or moderately curved line at humeral angle (Fig. 30.7b,c) 9

9(8) Male protarsomeres strongly asymmetrical, anterior lobes larger than posterior (Fig. 30.8e); northern Australia (Map 30.10) . . . . . *Sekaliporus*, 188

9′ Male protarsomeres symmetrical, anterior and posterior lobes similar (Fig. 30.8d) 10

10(9) Median lobe of male aedeagus bilaterally asymmetrical (Fig. 30.9a); female with apicolateral margins of elytra distinctly flanged (Fig. 30.10a); southwestern Australia (Map 30.3). . . . . *Brancuporus*, 184

10′ Median lobe of male aedeagus bilaterally symmetrical (Fig. 30.9b); female with apicolateral margins of elytra not flanged (Fig. 30.10b); southern Australia, New Zealand, and New Guinea (Map 30.1). . . . . *Antiporus*, 182

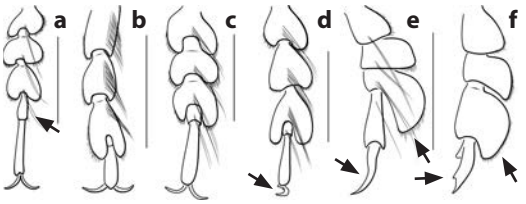


Fig. 30.8. Sternopriscina male protarsi. **a**, *Necterosoma penicillatum*. **b**, *Chostonectes gigas*. **c**, *Barretthydrus tibialis*. **d**, *Antiporus gilbertii*. **e**, *Sekaliporus kriegi*. **f**, *Tiporus josepheni*. Scales = 0.5mm (a,b,d) and 0.25mm (c,e).

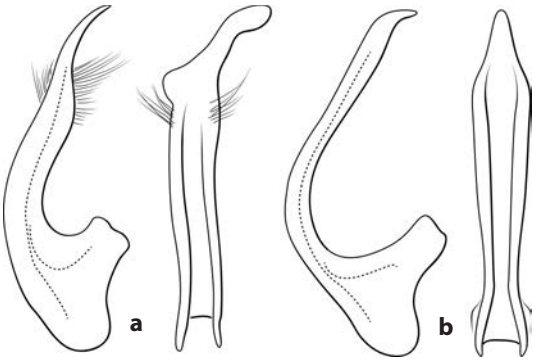


Fig. 30.9. Sternopriscina male median lobes, right lateral and ventral aspects. **a**, *Brancuporus pennifoldae*. **b**, *Antiporus blakeii*.

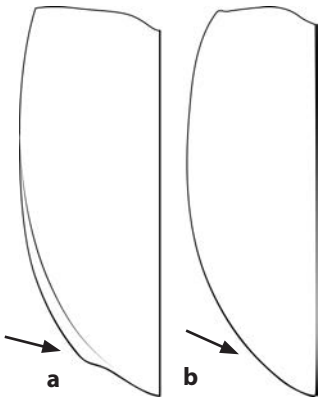


Fig. 30.10. Sternopriscina left elytra. **a**, *Brancuporus pennifoldae*. **b**, *Antiporus gilbertii*.

Genus *Antiporus* Sharp, 1882

Body Length. 3.4–6.5mm.

Diagnosis. *Antiporus* is very similar to *Brancuporus*, *Tiporus,* and *Sekaliporus* in having males with a single protarsal claw and reduced protarsomeres (Fig. 30.8d) as well as general overall similarity. *Antiporus* differs in having the combination of: (1) the metacoxal lines relatively far apart and more divergent; (2) the lateral elytral carina not abruptly bent near the humeral angle (Fig. 30.7b); (3) males with four distinctive protarsomeres that are approximately symmetrical with the anterior and posterior lobes similar (Fig. 30.8d); (4) the male median lobe bilaterally symmetrical (Fig. 30.9b); and (5) females without distinctive flanges or expansion on the apicolateral margins of the elytra (Fig. 30.10b). Male legs are often strongly modified with the protibia emarginate or toothed and some species have the metafemur with a prominent tooth along the ventral margin. Specimens are variable in size and coloration from nearly concolorous to variously maculate (Fig. 30.11).

Fig. 30.11. *Antiporus gilbertii*. Scale = 1.0mm.

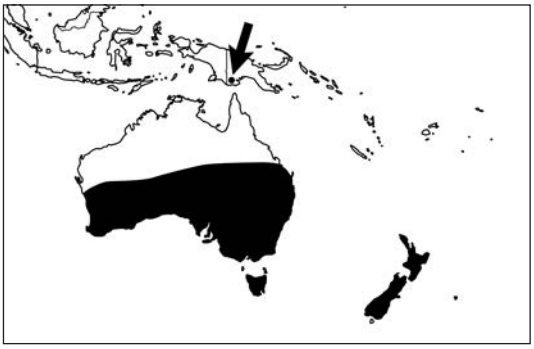
Fig. 30.12. *Barretthydrus tibialis*. Scale = 1.0mm.

Classification. The genus is closely related to *Brancuporus*, *Tiporus*, and *Sekaliporus* (Watts, 1997b; Hendrich *et al*., 2014; Toussaint *et al*., 2015b).

Diversity. Fifteen species are currently placed in *Antiporus* after two were recently moved to *Brancuporus* (Hendrich *et al*., 2014). Watts (1978) revised the species, but there have been several described since then (Watts, 1997b; Watts and Pinder, 2000; Hendrich, 2001).

Natural History. *Antiporus* occur in a variety of habitats, including ponds and slow streams, and can often be common in places with extensive vegetation. Larvae have been described (Alarie and Delgado, 1999; Alarie and Watts 2004).

Distribution. Species occur across most of southern Australia and throughout New Zealand (Map 30.1). There is one record of a teneral, unidentified specimen from southern New Guinea (Map 30.1, Balke, 1995b).



Map 30.1. Distribution of *Antiporus*.

Genus *Barretthydrus* Lea, 1927

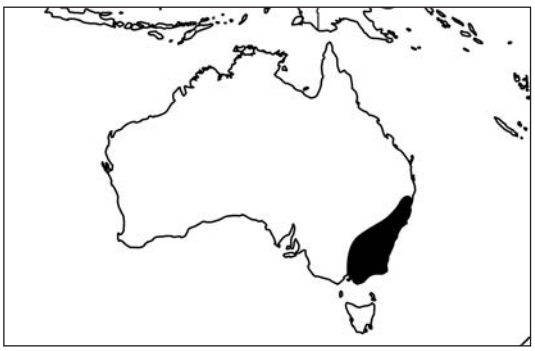
Body Length. 4.2–4.5mm.

Diagnosis. These are Sternopriscina with the following character combination: (1) the lateral body margins are somewhat discontinuous between the pronotum and elytron, and the body is robust but elongate oval (Fig. 30.12); (2) the elytron has four distinctive longitudinal grooves (Fig. 30.12); (3) the anterior surface of the metatibiae distinctly punctate; (4) the pro- and mesotarsi are pseudotetramerous with tarsomere IV short and hidden in the lobes of III (Fig. 30.8c); (5) males have two protarsal claws (Fig. 30.8c); and (6) the elytral epipleuron ends anteriorly in an oblique margin (Fig. 30.7a). Specimens are black with red dorsal maculae (Fig. 30.12).

Classification. The genus was recovered as sister to *Sternopriscus* by Toussaint *et al*. (2015b).

Diversity. There are only three species in this genus, and the group was revised by Watts (1978).

Natural History. Specimens mainly live in areas of



Map 30.2. Distribution of *Barretthydrus*.

vegetation in clear mountain streams.

Distribution. These species are known only from streams in the Great Dividing Range in Victoria and New South Wales, Australia (Map 30.2).

Genus *Brancuporus* Hendrich, Toussaint, and Balke, 2014

Body Length. 3.0–3.4mm.

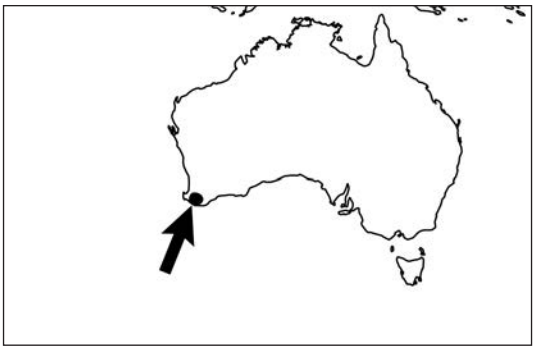
Diagnosis. *Brancuporus* are very similar to *Antiporus* in having males with a single protarsal claw and four protarsomeres as well as general overall similarity. *Brancuporus* differ in having the combination of (1) the male median lobe bilaterally asymmetrical (Fig. 30.9a) and (2) females with the apicolateral margins of the elytra distinctly flanged (Fig. 30.10a). The male protarsal claws are variously modified, and the male metafemur is expanded and sometimes toothed medially. Specimens are robust and evenly colored (Fig. 30.13).

Classification. The genus is closely related to *Antiporus*, *Tiporus*, and *Sekaliporus* (Hendrich *et al*., 2014; Toussaint *et al*., 2015b).

Diversity. Two species are currently placed in *Brancuporus*, *B. pennifoldae* (Watts and Pinder) and *B. gottwaldi* (Hendrich), both previously placed in *Antiporus*. The genus was treated by Hendrich *et al.* (2014) and the original species descriptions (Watts and Pinder, 2000; Hendrich, 2001a).

Natural History. Specimens occur in peatlands and seasonal swamps (Hendrich *et al*., 2014).

Distribution. The two species of *Brancuporus* are found in southwestern Australia (Hendrich *et al.*, 2014) (Map 30.3).



Map 30.3. Distribution of *Brancuporus*.

Genus *Carabhydrus* Watts, 1978

Body Length. 1.6–3.6mm.

Diagnosis. Members of this group are quite characteristic within Sternopriscina with the habitus elongate and the lateral outline strongly discontinuous between the pronotum and elytron (Fig. 30.14). There are two longitudinal grooves along the disc of each elytron (Fig. 30.14), and the scutellum is visible with the elytra closed (Fig. 30.14). Also, the metacoxal process is apressed to the body surface and the metacoxae are fused to the base of the abdomen. Several species in the group are subterranean with the characteristic depigmentation, reduced eyes, and other attributes of dytiscids with that lifestyle.

Classification. This genus was originally erected

Fig. 30.13. *Brancuporus gottwaldi*. Scale = 1.0mm.

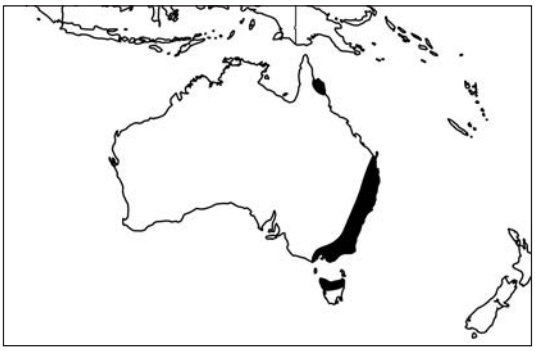
Fig. 30.14. *Carabhydrus niger*. Scale = 1.0mm.

and placed within its own tribe, Carabhydrini Watts, based on the very unique combination of features associated with this group, though these were later shown to be derived within Sternopriscina (Ribera *et al.*, 2008; Miller and Bergsten, 2014a), and the tribe was synonymized by Miller and Bergsten (2014a) although treated in Hydroporini already by Watts *et al.* (2007) and Hendrich and Watts (2009). *Carabhydrus* was recovered as sister to *Barretthydrus* + *Sternopriscus* by Toussaint *et al*. (2015b).

Diversity. There are currently 10 species recognized in *Carabhydrus*, and these were revised by Hendrich and Watts (2009).

Natural History. These are rheophilic beetles with most species occurring in gravel regions of streams and some in subterranean habitats (Watts *et al.*, 2007; Leys and Watts, 2008; Leys *et al.*, 2010).

Distribution. *Carabhydrus* are found in eastern Australia in the Great Dividing Range and north in Queensland (Map 30.4).



Map 30.4. Distribution of *Carabhydrus*.

Genus *Chostonectes* Sharp, 1880

Body Length. 3.5–6.3mm.

Diagnosis. *Chostonectes* is similar to *Megaporus* in the large size of many specimens and the impunctate anterior surface of the metatibia (Fig. 30.5a), but they differ from members of that genus in having the metafemur more slender and the anterodorsal angle produced and angulate (Fig. 30.5a). Watts (1978) emphasized the nature of the anteroventral angle of the metafemur as a diagnostic features, but Balke (1995b) reexamined this character and instead emphasized the shape of the anterodorsal angle, though he had not examined the character comprehensively. Specimens are medium in size to quite large and generally attractively marked (Fig. 30.15).

Fig. 30.15. *Chostonectes gigas*. Scale = 1.0mm.

Classification. The group is closely related to *Megaporus* (Balke, 1995b; Hendrich *et al.*, 2014; Miller and Bergsten, 2014a). The two genera are not easily diagnosed from each other, and were in fact recovered as paraphyletic with respect to *Megaporus* by Toussaint *et al*. (2015b).

Diversity. The six species in this genus were mostly revised by Watts (1978) with a key to all species, including a new one, presented by Balke (1995b).

Natural History. *Chostonectes* are mainly found in ponds and slow streams, often those with much vegetation.

Distribution. Species are found across eastern Australia and New Guinea (Map 30.5).

Map 30.5. Distribution of *Chostonectes*.

Genus *Megaporus* Brinck, 1943

Body Length. 4.9–6.3mm.

Fig. 30.16. *Megaporus howittii*. Scale = 1.0mm.

Diagnosis. This genus is very similar to *Chostonectes* in being usually large in size (for hydroporines) and having the anterior surface of the metatibia impunctate (Fig. 30.5b), but *Megaporus* has the metafemur broader and the anterodorsal angle broadly rounded (Fig. 30.5b). Watts (1978) used the anteroventral angle of the metafemur as a diagnostic character separating *Chostonectes* and *Megaporus*. Balke (1995b) reexamined this character and regarded the anterodorsal angle as a better diagnostic feature, though his examination was not comprehensive. Specimens are large and range from concolorous to distinctly maculate (Fig. 30.16).

Classification. The group is closely related to *Chostonectes* (Balke, 1995b; Hendrich *et al*., 2014; Miller and Bergsten, 2014a; Toussaint *et al*., 2015b; see above under *Chostonectes*).

Diversity. There are 11 species currently in *Megaporus*. The species were revised by Watts (1978).

Natural History. *Megaporus* are found in a large number of habitats, but especially in ponds and stream margins with vegetation.

Distribution. *Megaporus* are found throughout Australia, including Tasmania, and in New Guinea and on New Caledonia (Map 30.6).

Fig. 30.17. *Necterosoma penicillatum*. Scale = 1.0mm.

Genus *Necterosoma* MacLeay, 1871

Body Length. 3.3–5.4mm.

Diagnosis. *Necterosoma* are Sternopriscina with the following character combination: (1) the lateral body margins somewhat discontinuous between the pronotum and elytron, with the body elongate oval (Fig. 30.17); (2) the elytron without longitudinal grooves (Fig. 30.17); (3) the pro- and mesotarsi distinctly pentamerous with IV relatively elongate and conspicuous (Fig. 30.8a); (4) the overall length >3.3mm; (5) the metacoxal cavities closely approximated (Fig. 30.4b); and (6) the metacoxal process with the posterior margin with a V-shaped medial emargination (Fig. 30.4b). Specimens are often longitudinally fasciate (Fig. 30.17), and males often have the profemur enlarged compared to females

Map 30.6. Distribution of *Megaporus*.

Map 30.7. Distribution of *Necterosoma*.

Fig. 30.18. *Paroster* species. **a**, *P. nigroadumbratus*. **b**, *P. napperbyensis*. **c**, *P. macrocephalus*. **d**, *P. caecus*. Scales = 1.0mm. Photos b and c thanks to C. H. S. Watts and H. Hamon, South Australia Museum, Adelaide, Australia. Used with permission.

and the protibia medially emarginate (Fig. 30.3).

Classification. A preliminary phylogeny of *Necterosoma* based on the mitochondrial gene CO1 was explored by Balke *et al*. (2013a). Several species in this genus seems to be the result of relatively recent diversification (Hendrich *et al*., 2010).

Diversity. Twelve species are recognized in *Necterosoma*. The group was revised by Watts (1978), though several additional species were described after that from Australia, New Caledonia, and West Timor of Indonesia.

Natural History. *Necterosoma* are found in a wide range of aquatic habitats from ponds to streams and can be extremely abundant.

Distribution. Species are known from throughout Australia, New Caledonia, and Timor (Map 30.7).

Genus *Paroster* Sharp, 1882

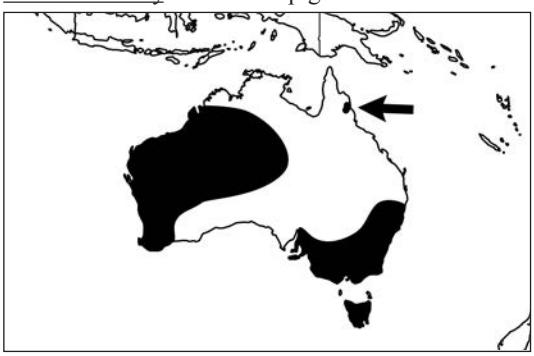
Body Length. 1.0–4.2mm.

Diagnosis. These are the only Sternopriscina with the elytral epipleuron abruptly narrowed medially and narrow apically (Fig. 30.6a). The other members of the subtribe have the elytral epipleuron broad throughout most of its length (e.g., Fig. 30.6b). Epigean members of the group are small to extremely small (<4mm). In addition: (1) the metacoxal cavities are exposed and separated; (2) the anterior surface of the metatibia is impunctate; (3) the pro- and mesotarsi are pseudotetramerous with tarsomere IV short and hidden in the lobes of III; (4) the elytral epipleuron has a transverse carina at the humeral angle (Fig. 30.6a); and (5) the body is elongate oval with the lateral margins approximately continuous between the pronotum and elytron (Fig. 30.18a). Most members of this group are subterranean, however, and they have many of the typical characteristics of this lifestyle, including microphthalmy or anophthalmy, depigmentation, reduced flight wings, etc. (Fig. 30.18b,c). This, and the addition of species formerly in *Terradessus* (20.18d, see below), complicates general diagnostics for the group.

Classification. The subterranean species were originally placed in the genus *Nirripirti* Watts and Humphreys, until it became clear that these taxa were derived within the epigean *Paroster* and the name was synonymized (Leys and Watts, 2008). Most recently, Touissant *et al.* (in press-b) discovered that *Terradessus* Watts also belong to *Paroster*. The relationship to other Sternopriscina genera is uncertain.

Diversity. This genus contains 50 recognized species of which only 7 are more typical, epigean species, two are likely terrestrial and the rest are all subterranean and were described in recent years from paleodrainages in western Australia (Watts and Humphreys, 2004; 2006; 2009; Watts *et al.*, 2008; Leys *et al.*, 2010).

Natural History. The few epigean members of the



Map 30.8. Distribution of *Paroster*.

group inhabit seeps and small streams. The subterranean species are from aquifers and paleodrainages. Two species, previously placed in *Terradessus*, may be among the few terrestrial species in Dytiscidae.

Distribution. Species are known mainly from southern and western Australia (Map 30.8).

Genus *Sekaliporus* Watts, 1997

Body Length. 3.1–3.8mm.

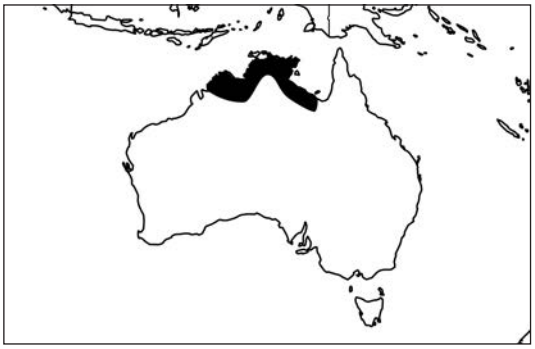
Diagnosis. *Sekaliporus* is very similar to *Brancuporus*, *Antiporus,* and *Tiporus* in having males with a single protarsal claw and reduced protarsomeres as well as general overall similarity. *Sekaliporus* differs in having the combination of: (1) the metacoxal lines close together and subparallel; (2) the elytral carina not abruply bent near the humeral angle (Fig. 30.7c), and; (3) males with four distinctive, asymmetrical protarsomeres with the anterior margins extended in conspicuous lobes (Fig. 30.8e). The male legs are otherwise unmodified, but usually are variously shaped in *Antiporus* and *Tiporus*.

Classification. Watts (1997a) thought the genus is closely related to *Antiporus* and *Tiporus*, and Toussaint *et al*. (2015b) found *Sekaliporus* sister to *Tiporus*.

Diversity. There are two species in the genus, *S. kriegi* Watts (Fig. 30.19) and *S. davidi* Hendrich and Balke, which can be identified by characters given in Hendrich and Balke (2015).

Natural History. This is a lotic genus restricted to slow flowing rivers, streams and creeks in tropical, often forested areas (Watts, 1997a; Hendrich and Balke, 2015). Both species have been documented flying (Hendrich and Balke, 2015).

Distribution. *Sekaliporus* are known from coastal northern Australia (Map 30.10).



Map 30.10. Distribution of *Sekaliporus*.

Genus *Sternopriscus* Sharp, 1880

Body Length. 1.8–4.5mm.

Diagnosis. These are Sternopriscina with the following character combination: (1) the lateral body margins somewhat discontinuous between the pronotum and elytron and the body elongate oval (Fig. 30.20); (2) the elytron without longitudinal grooves (Fig. 30.20); (3) the pro- and mesotarsi distinctly pentamerous with tarsomere IV relatively elongate and conspicuous; (4) overall length < 4.5mm; (5) the metacoxal cavities distinctly separated (Fig. 30.4a); and (6) the metacoxal process medially with the pos-

Fig. 30.19. *Sekaliporus kriegi* Scale = 1.0mm.

Fig. 30.20. *Sternopriscus clavatus.* Scale = 1.0mm.

terior margin extending posteriorly in a V-shaped production (Fig. 30.4a). Specimens are typically tan to black with variable, fasciate markings dorsally (Fig. 30.20), and males often have the medial antennomeres strikingly modified with lateral expansions in a species-specific shape (Fig. 30.20) and the protibia with a distinctive medial emargination (like in Fig. 30.3).

Classification. Like *Necterosoma*, *Sternopriscus* contains a number of genetically closely related species that likely diversified relatively recently (Hendrich *et al*., 2010). The closest relative seems to be *Barretthydrus* (Toussaint *et al*., 2015b).

Diversity. There are currently 29 species in *Sternopriscus*. The group was revised in a modern context by Hendrich and Watts (2004) with additional species added later also by Hendrich and Watts (2007).

Natural History. *Sternopriscus* occur in nearly all typical aquatic habitats in Australia. They can often be very abundant, and occasionally come to lights. The evolutionary history and recent diversification of the group was studied by Hawlitschek *et al.* (2012).

Distribution. *Sternopriscus* occur throughout Australia (Map 30.11). There is one record from Irian Jaya, New Guinea (Balke, 1995b), but Hendrich and Watts (2004) questioned this record.

Map 30.11. Distribution of *Sternopriscus*.

Genus *Tiporus* Watts, 1985

Body Length. 3.2–5.6mm.

Diagnosis. *Tiporus* is very similar to *Antiporus*, *Brancuporus,* and *Sekaliporus* (Fig. 30.21) in having males with a single protarsal claw and reduced protarsomeres as well as general overall similarity.

Fig. 30.21. *Tiporus josepheni*. Scale = 1.0mm.

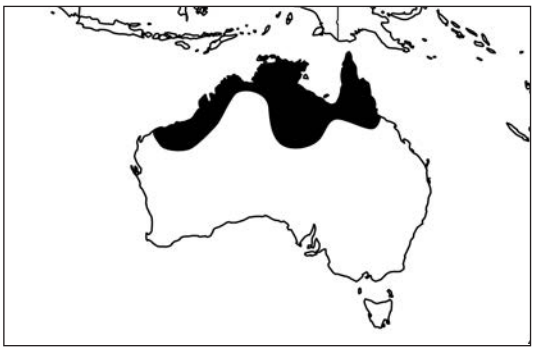
Tiporus differs in having the combination of: (1) the metacoxal lines farther apart and divergent; (2) the elytral carina abruptly bent near the humeral angle (Fig. 30.7d); and (3) males with only three distinctive protarsomeres with the single claw arising from the apex of the third, and these protarsomeres strongly asymmetrical with the anterior margins extended in conspicuous lobes (Fig. 30.8f). The male legs are often further modified with the protibia emarginate or toothed in various ways, though not in all species.

Classification. This genus concept was originally conceived with the preoccupied name *Hypodes* Watts (1978), and later replaced by *Tiporus* Watts (1985). The genus is closely related to *Antiporus* and especially *Sekaliporus* (Watts, 1997b; Toussaint *et al*., 2015b).

Diversity. Twelve species are currently assigned to *Tiporus*, which are treated by Watts (1978; 2000).

Natural History. Many species occur in temporary pools, the margins of slow, lowland streams, and similar habitats.

Distribution. *Tiporus* species are found in northern Australia (Map 30.12).



Map 30.12. Distribution of *Tiporus*.

31. Tribe Vatellini

Body Length. 3.2–7.3mm.

Diagnosis. Vatellini are characterized by the following: (1) the metepisternum is externally separated from the mesocoxa (Fig. 31.1a); (2) the prosternal process does not reach the metaventrite (the mesocoxae are contiguous) (Fig. 31.1b); (3) abdominal sternite VI has an invaginated, heavily sclerotized gland system (the "speleum") (Figs. 31.1d–f,2, Miller, 2005a); and (4) females have an apically expanded and broadly truncated process at the apex of the spermatheca (Fig. 31.6). Members of this tribe are among the most distinctive within the subfamily and are characterized by a large number of particularly unusual apomorphies. They have long legs and an elongate, often somewhat cylindrical body that is slightly to strongly discontinuous laterally where the pronotum meets the elytron (Figs. 31.7,8).

Classification. The group historically included four genera, *Vatellus*, *Macrovatellus* Sharp, *Derovatellus*, and *Mesovatellus* Trémouilles. A recent revision by Miller (2005a) included synonymy of *Macrovatellus* with *Vatellus* and *Mesovatellus* with *Derovatellus*. Relationships of this tribe with other members of Hydroporinae are among the most ambiguous of any in the subfamily. In the recent analysis by Miller and Bergsten (2014a) the tribe is resolved as sister to a large clade including several other tribes with moderately strong support, but morphological and molecular evidence for relationships of Vatellini with other diving beetles is not convincing.

Diversity. The tribe includes two genera, *Vatellus* and *Derovatellus*.

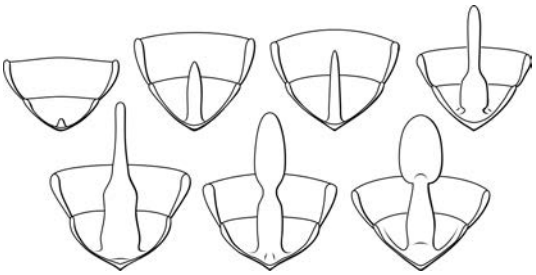


Fig. 31.2. Vatellini species, variation in speleum shape.

Natural History. Members of the group are found in tropical marshes and ponds with dense vegetation. Members of *Derovatellus* can be very abundant, but *Vatellus* are often much more rarely collected. The function of the unusual gland system in the abdomen (the "speleum," Fig. 31.1d–f) is unknown, but it is variable in shape from species to species in each genus (Fig. 31.2). Most dytiscids with shortened prosternal processes and contiguous mesocoxae like those in Vatellini (Fig. 31.1b) are lotic, whereas vatellines are instead lentic. This group is quite different from most dytiscids in body form and unique morphological synapomorphies of unknown function, making these very compelling beetles for future study.

Distribution. Collectively the group occurs in the Afrotropical region and from the extreme southern United States through Mexico and Central America and throughout lowland South America to Argentina with only a single additional species of *Derovatellus* in Southeast Asia.

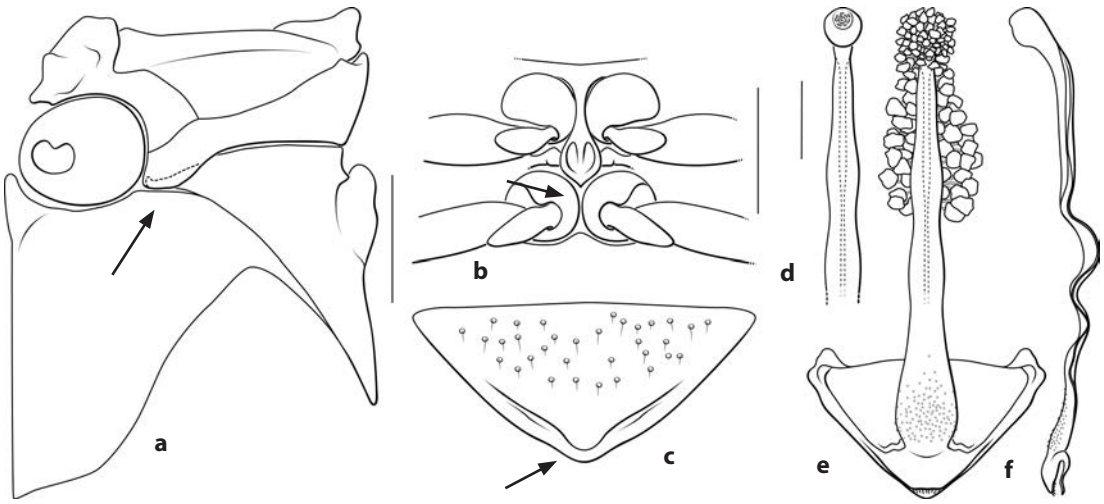


Fig. 31.1. Vatellini features. **a**, *Vatellus grandis*, left thoracic sclerites. **b**, *Derovatellus lentus*, prosternal process, and bases of pro- and mesolegs. **c**, *V. maculosus*, last abdominal sternite, lobed opening to speleum. **d**, *D. lentus* anterior part of speleum. **e**, *D. lentus* speleum and abdominal ventrite VI. **f**, *D. lentus* speleum, lateral aspect. Scales = 1.0mm (a,b) and 0.25mm (d–f).

Key to the Genera of Vatellini

1 Pronotum not cordate, margins variously curved but widest at or posterior to middle (Fig. 31.7); metacoxal lines moderately approximated throughout length, not or only slightly divergent anteriorly (Fig. 31.3a); metatrochanter with ventral (posterior) margin evenly curved, not emarginate and without prominent basal, circular lobe (Fig. 31.4a); size smaller, total length = 3.2–5.0mm; male median lobe not basally extended (Fig. 31.5a); female spermatheca elongate, tubular, medially angulate (Fig. 31.6a); apical margin of ventral apex of orifice of speleum not lobed; southeastern Nearctic, Neotropical, Afrotropical, and Southeast Asia (Map 31.1) . . . . . *Derovatellus*, 191

1′ Pronotum variously cordate, widest anterior to middle (Fig. 31.8); metacoxal lines generally closely approximated posteriorly, strongly divergent anteriorly (Fig. 31.3b); ventral (posterior) margin of metatrochanter with prominent medial emargination and with prominent basal, circular lobe that extends medially over surface of metacoxa with leg in anterior position (Fig. 31.4b); size larger, total length = 4.6–7.3mm; male median lobe strongly extended basally (Fig. 31.5b); female spermatheca globular, subspherical (Fig. 31.6b); apical margin of ventral apex of orifice of speleum distinctly lobed (Fig. 31.1c); southern Nearctic and Neotropical (Map 31.2) . . . . *Vatellus*, 192

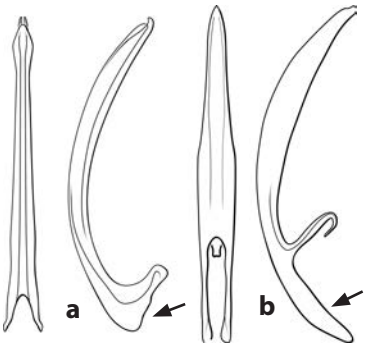


Fig. 31.5. Male median lobe, ventral and right lateral aspects. **a**, *Derovatellus lentus*. **b**, *Vatellus maculosus*.

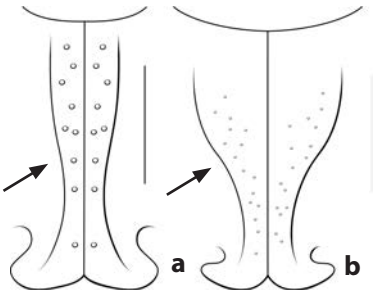


Fig. 31.3. Metacoxal lines. **a**, *Derovatellus lentus*. **b**, *Vatellus maculosus*. Scales = 0.25mm.

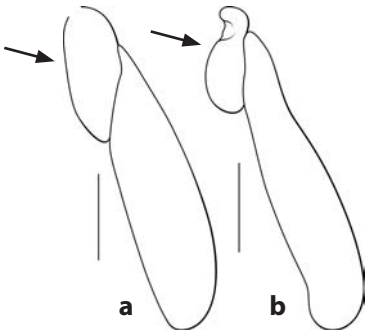


Fig. 31.4. Metatrochanter and metafemur. **a**, *Derovatellus lentus*. **b**, *Vatellus maculosus*. Scales = 0.25mm (a) and 0.50mm (b).

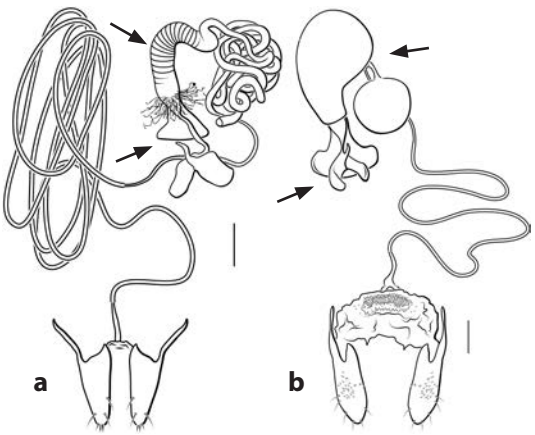


Fig. 31.6. Female reproductive tract showing triangular spermathecal process and spermathecal shape. **a**, *Derovatellus lentus*. **b**, *Vatellus maculosus*. Scales = 0.1mm.

Genus *Derovatellus* Sharp, 1882

Body Length. 3.2–5.0mm.

Diagnosis. Members of this genus are differentiable from the other extant genus of the tribe, *Vatellus*, by the combination of: (1) the lateral body outline not as strongly discontinuous, the pronotum generally broadest at the middle or posterior to the middle (Fig. 31.7); (2) the metacoxal lines closely approximated

Fig. 31.7. *Derovatellus lentus*. Scale = 1.0mm.

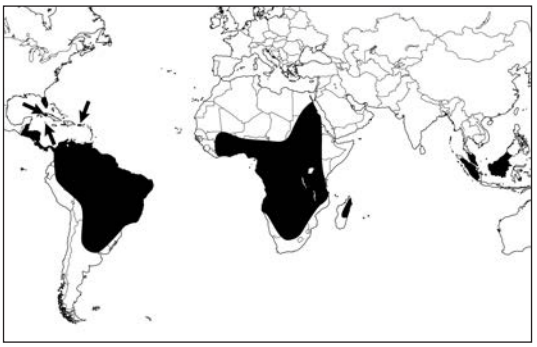
(Fig. 31.3a); (3) the male lateral lobes and median lobe without strongly extended basal portions (Fig. 31.5a); (4) the female spermatheca elongate, slender, and medially bent (Fig. 31.6a); (5) metatrochanter not modified (Fig. 31.4a); and (6) the apical margin of the ventral apex of the opening to the speleum not distinctly lobed. Members of *Derovatellus* are generally smaller (<5mm) than most *Vatellus* (>4.6mm).

Classification. Historically, *Derovatellus* was divided into two subgenera, *Derovatellus s. str.* and *D.* (*Varodetellus*) Biström, but these were found to not be mutually monophyletic in a recent cladistic analysis (Miller, 2005a). The genus *Mesovatellus* Trémouilles was also synonymized with *Derovatellus* by Miller (2005a).

Diversity. Currently, there are 42 species in *Derovatellus*. African species were revised by Biström (1979), with numerous subsequent related papers (Biström, 1980; 1981; 1982a; 1983c; 1984b; 1986a; 2003; Biström and Roughley, 1982) and the New World and Southeast Asian species were revised by Miller (2005a).

Natural History. *Derovatellus* are found in marshes and ponds, usually with dense vegetation. They can be quite abundant in certain circumstances. They readily come to lights. Larvae have been described by Spangler (1966).

Distribution. *Derovatellus* has an unusual distribution with species found mainly in lowland Central and South America (including southern Florida) and central Africa, including one species, *D. marmottani* Guignot, on Madagascar (Map 31.1). A single additional species, *D. orientalis* Wehncke, is found in Borneo, Sumatra, and peninsular Malaysia (Map 31.1).



Map 31.1. Distribution of *Derovatellus*.

Genus *Vatellus* Aubé, 1837

Body Length. 4.6–7.3mm.

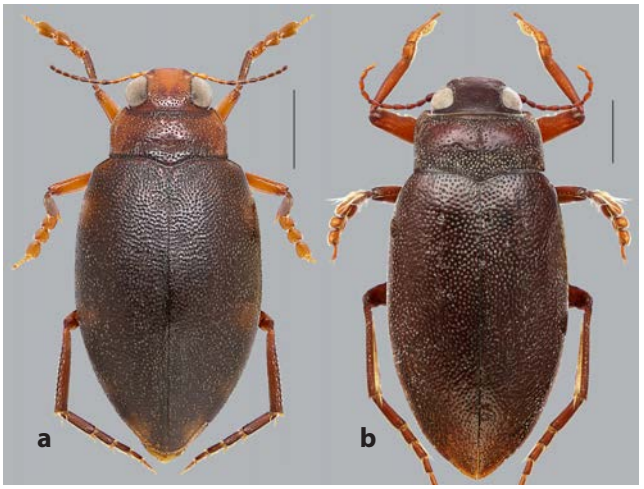


Fig. 31.8. *Vatellus* species. **a**, *V. haagi*. **b**, *V. grandis*. Scales = 1.0mm.

Diagnosis. Members of *Vatellus* are differentiable from the other extant genus of the tribe, *Derovatellus*, by the combination of: (1) the lateral body outline more strongly discontinuous, pronotum broadest anterior to middle (Fig. 31.8); (2) the metacoxal lines approximated posteriorly, and anteriorly moderately to strongly divergent (Fig. 31.3b); (3) the male median and lateral lobes strongly extended basally, elongate (Fig. 31.5b); (4) the female spermatheca subspherical, only slightly elongate in some species (Fig. 31.6b); (5) the metatrochanter large and strongly offset (Fig. 31.4b); and (6) the apical margin of the ventral apex of the opening to the speleum distinctly, but variably, lobed (Fig. 31.1c). Members of *Vatellus* are generally larger (> 4.6mm) than most *Derovatellus* (< 5.0mm).

Classification. Most of the members of this group were described in the genus *Macrovatellus* with only one species placed in *Vatellus*. However, these two genus concepts overlap, and the two names were synonymized by Miller (2005a).

Diversity. *Vatellus* currently includes 15 species. They were revised by Miller (2005a).

Natural History. Specimens are generally collected in marshes and ponds with dense vegetation and sometimes forest pools. They rarely come to lights. Unlike *Derovatellus*, specimens of *Vatellus* are more rare, and more rarely collected in long series. Larvae have been described by Michat and Torres (2005a) and Spangler (1963).

Distribution. Species of *Vatellus* occur from southern Texas, USA, south through Mexico and Central America and throughout lowland South America south to Argentina (Map 31.2).

Map 31.2. Distribution of *Vatellus*.

32. Tribe Methlini

Body Length. 2.0–6.8mm.

Diagnosis. Methlini are Hydroporinae characterized by: (1) the metafemur extending to the metacoxal lobe along the dorsal margin (Fig. 32.1a) and (2) terga VII and VIII modified, tergum VIII posteriorly acute and with dorsal and ventral lobes, the dorsal lobe posteriorly modified into a trifid structure with a pair of long apodemes extending anteriorly, and tergum VII also with shorter anterior apodemes. The posterior apex of the abdomen and elytra is acuminate (Fig. 32.1b). Members of the New World genus *Celina* are characterized additionally by an externally visible and large scutellum (with the elytra closed; Fig. 31.2a), which is unique among Hydroporinae genera. Other genera — e.g., *Carabhydrus* and *Hydrocolus* — have a small portion of the scutellum visible, but not to the degree of *Celina*.

Classification. Sharp (1882) recognized close similarity between the genera *Methles* and *Celina*, and since then they have been recognized as closely related. The group has been occasionally recognized at the family rank (e.g., Omer-Cooper, 1958b; Franciscolo, 1966; Bilardo and Rocchi, 1990; Trémouilles, 1995), but it is clearly nested among Hydroporinae (e.g., Miller and Bergsten, 2014a). Wolfe (1985; 1988) proposed potential synapomorphies for Methlini and suggested that the group exhibits a number of plesiomorphies within Hydroporinae that make them close to *Laccornis*, *Laccornellus* and *Canthyporus*. He also thought Methlini and *Hydrovatus* could be sister groups based on similar features in the abdominal apex. Ribera *et al*. (2008) found a monophyletic Methlini sister to *Peschetius*, but Miller and Bergsten (2014a) found the tribe monophyletic with strong support but placed with weak support as sister to a clade with Pachydrini, Hydrovatini and Hygrotini.

Diversity. The tribe includes two genera, *Methles* and *Celina.*

Natural History. No functional explanation has been shown for the distinctly acuminate apex of the body (Figs. 32.1b,3,4). Possibly it is used for piercing plant tissues to access air-filled vacuoles for respiration without having to surface (Wolfe, 1988).

Distribution. The two genera in this group occur in eastern and southern North America south throughout Central America, lowland South America (*Celina*), and Africa to India (*Methles*).

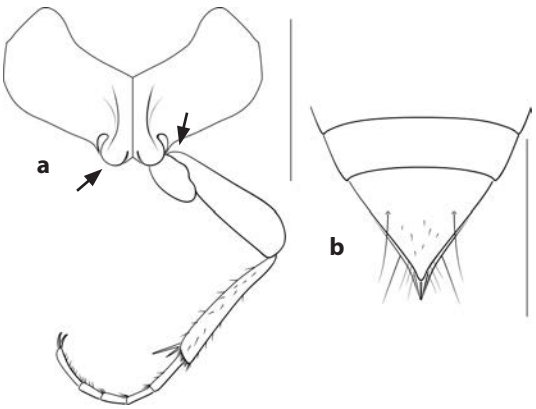


Fig. 32.1. Methlini features. **a**, *Celina hubbelli*, metacoxa and left metaleg. **b**, *Methles cribratellus*, apex of abdomen, ventral aspect. Scales = 1.0mm.

Key to the Genera of Methlini

1 Scutellum visible with elytra closed (Fig. 32.2a); Nearctic and Neotropical (Map 32.1) . . . . . .*Celina*, 194

1′ Scutellum concealed with elytra closed (Fig. 32.2b); Afrotropical through middle east to India (Map 32.2) . . . . . .*Methles*, 195

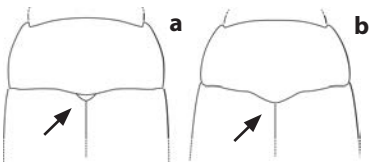


Fig. 32.2. Methlini dorsal surface. **a**, *Celina hubbelli.* **b**, *Methles cribratellus.*

Genus *Celina* Aubé, 1837

Body Length. 2.0–6.8mm.

Diagnosis. Within Methlini, this genus differs from *Methles* in having a large, exposed scutellum (Figs. 32.2a,3), which is unique, also, among Hydroporinae. In other respects, the two genera are similar.

Classification. Because of the exposed scutellum combined with other features unique to Hydropori-

Fig. 32.3. *Celina hubbelli*. Scale = 1.0mm.

nae, this genus has had a volatile history of classification. For at least some of its history, it has been in its own subfamily (e.g., Branden, 1885; Falkenström, 1938). However, Wolfe (1985; 1988) convincingly associated it with other Hydroporinae based on cladistic analysis, together with *Methles*, in a position as sister to much of the group.

Diversity. There are currently 34 *Celina* species. The North American species were keyed by Young (1979b). The Neotropical species have never been revised and are in much need of treatment.

Natural History. Specimens are generally collected in lentic habitats with vegetation, though they may be found in slow lotic situations or forest pools. They regularly come to lights at night. In some areas of lowland South America they can be one of the most abundant groups with multiple species occurring together. Larvae have been described (Spangler, 1974; Crespo, 1994).

Distribution. *Celina* are found in eastern North America from Quebec to Florida west to Texas and from California south throughout Central America and throughout lowland South America (Map 32.1).

Fig. 32.4. *Methles cribratellus*. Scale = 1.0mm.

Genus *Methles* Sharp, 1882

Body Length. 2.3–3.6mm.

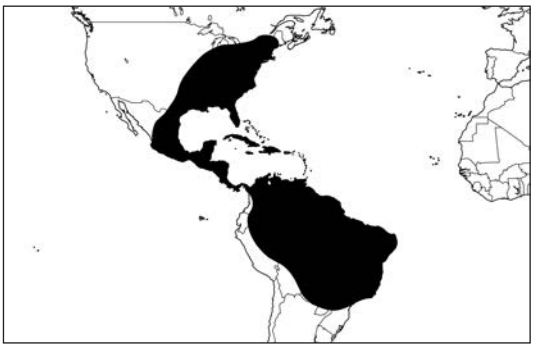
Diagnosis. Within Methlini, this genus differs from *Celina* in having the scutellum concealed with the elytra closed (Figs. 32.2b,4). In other respects, the two genera are similar.

Classification. The group has been associated with *Celina* for most of its history (Sharp, 1882).

Diversity. There are eight species and one subspecies in the genus. The group has not been revised entirely, but the African species can be identified using Guignot (1959a) and the Indian by Vazirani (1970).

Natural History. Specimens are typically collected in vegetated ponds, marshes, lake margins, and, occasionally, streams. They regularly come to lights.

Distribution. *Methles* has species throughout Africa, southern Europe, and east to India (Map 32.2).



Map 32.1. Distribution of *Celina*.

Map 32.2. Distribution of *Methles*.

33. Tribe Hydrovatini

Body Length. 1.6–6.2mm.

Diagnosis. This tribe is characterized by the following combination: (1) the elytral epipleuron has an oblique carina at the humeral angle (Fig. 33.1b; (2) the apex of the prosternal process is broad and triangular and laterally distinctly margined (Fig. 33.1b); (3) the metatarsal claws are equal in length (Fig. 33.1a,b); and (4) the metacoxal apices are incised on each side and subtend a narrowly or broadly rounded metacoxal lobe (Fig. 33.1a,b).

Classification. Sharp (1882) placed *Queda* and *Hydrovatus* together in a tribe, Hydrovatini, and they stayed this way until Wolfe (1985; 1988) presented evidence that *Hydrovatus* and members of the tribe Methlini (*Celina* and *Methles*) share many similarities that he considered plesiomorphic within the Hydroporinae. Biström (1990; 1996b) reviewed the morphological evidence and reached a different conclusion, that *Queda* and *Hydrovatus* indeed form a monophyletic group, though he thought Methlini may be sister to Hydrovatini. Monophyly of Hydrovatini (*Hydrovatus* + *Queda*) was corroborated also by Miller (2001c) and Miller *et al.* (2006), who found the tribe to be phylogenetically near Hygrotini and Hyphydrini. Ribera *et al.* (2008) did not include *Queda*, but found a monophyletic *Hydrovatus* sister to Vatellini. Most recently Miller and Bergsten (2014a) found a monophyletic Hydrovatini (*Hydrovatus* + *Queda*) with good support. There are no well-supported conclusions, however, about relationships between Hydrovatini and other tribes (Miller, 2001c; Ribera *et al.*, 2008; Miller and Bergsten, 2014a).

Diversity. The tribe includes two genera, *Hydrovatus* and *Queda.*

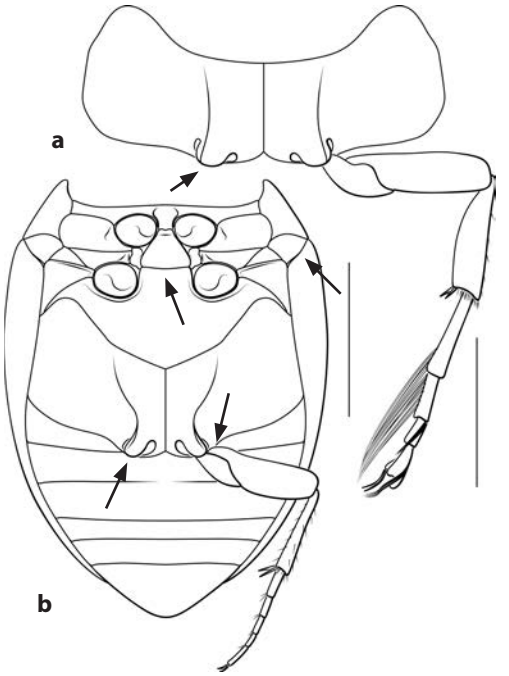


Fig. 33.1. Hydrovatini, ventral surfaces showing broad prosternal process, metacoxal incisions, and oblique transverse epipleural carina. **a**, *Queda youngi*, metacoxa and left metaleg. **b**, *Hydrovatus cardoni*, ventral surface except head. Scales = 1.0mm.

Natural History. Members of this group are found primarily in lentic waters with considerable vegetation. They often come to lights.

Distribution. Of the two genera, *Hydrovatus* is much more widespread and circumtropical, though most diverse in Africa to Southeast Asia. *Queda* is only found in South America, where there are only a few *Hydrovatus* species.

Key to the Genera of Hydrovatini

1 Anterior clypeal margin rounded to truncate, not bordered or only narrowly or weakly (Fig. 33.2a); labrum visible in part Fig. 33.2a); lateral incisions at apex of metacoxal process narrow and deep, lobes narrow and elongate (Fig. 33.1b); worldwide (Map 33.1) . . . . . .*Hydrovatus*, 197

1′ Anterior clypeal margin flattened and broadly bordered (Fig. 33.2b); labrum concealed (Fig. 33.2b); lateral incisions at apex of metacoxal process shallow and broad, lobes broad (Fig. 33.1a); Neotropical (Map 33.2). . .*Queda*, 198

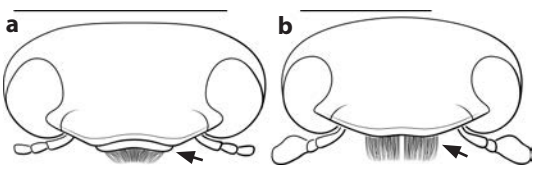


Fig. 33.2. Hydrovatini, head, anterior aspect. **a**, *Hydrovatus cardoni*. **b**, *Queda youngi*. Scales = 1.0mm.

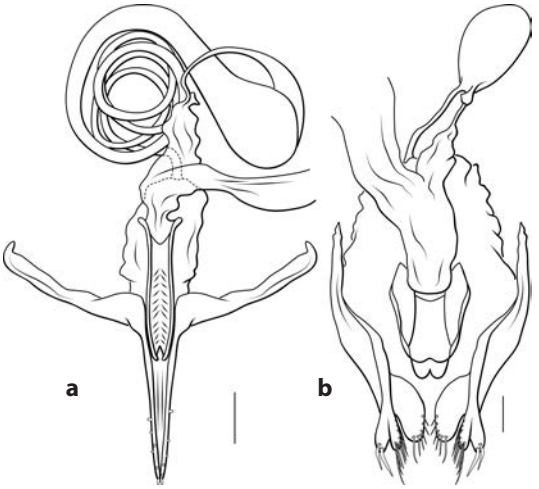
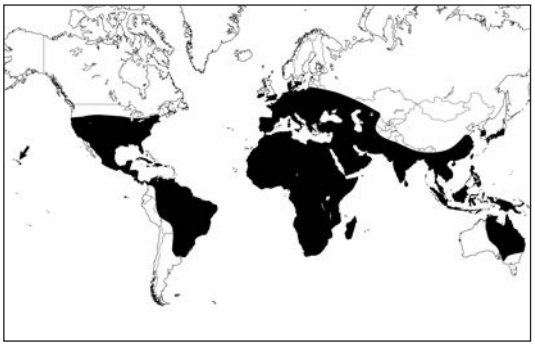


Fig. 33.3. Hydrovatini female reproductive tracts and ovipositors. **a**, *Hydrovatus pustulatus*. **b**, *Queda youngi*. Scales = 0.1mm.

Genus *Hydrovatus* Motschulsky, 1853

Body Length. 1.6–5.3mm.

Diagnosis. Within Hydrovatini, these species are easily diagnosed by the deeply incised metacoxal process with long, slender metacoxal lobes (Fig. 33.1b). The anterior clypeal margin is rounded or straight with a weak, narrow border or is unbordered (Fig. 33.2a). The female gonocoxae are together fused into a knife-like ovipositor with elongate lateral extensions at the base (Fig. 33.3a), a unique feature in all Dytiscidae. Specimens of most species are robust and globular with the posterior apex of the body (elytra and abdomen) acuminate (Fig. 33.4a). Some are somewhat more elongate (Fig. 33.4b). They range from concolorous (Fig. 33.4b) to distinctly maculate or fasciate (Fig. 33.4a).



Map 33.1. Distribution of *Hydrovatus*.

Classification. The sister-group relationship of *Hydrovatus* with *Queda* was supported by Miller and Bergsten (2014a).

Diversity. There are currently 208 species in this large genus, making it one of the largest in the family. Although diverse in species, many are extremely similar in general appearance and can be distinguished mainly by characters of the male genitalia. The entire group was treated in an impressive, monumental revision by Biström (1996b), though others have been described since (Biström, 1996c; 1999). The few South American species were treated by Trémouilles *et al.* (2005).

Natural History. Most species occur in well-vegetated ponds and slow streams, where they can often be found in large numbers, though in many cases they are represented by a diversity of species but low specimen numbers. The knife-shaped ovipositor (Fig. 33.3a) suggests they lay eggs endophytically,

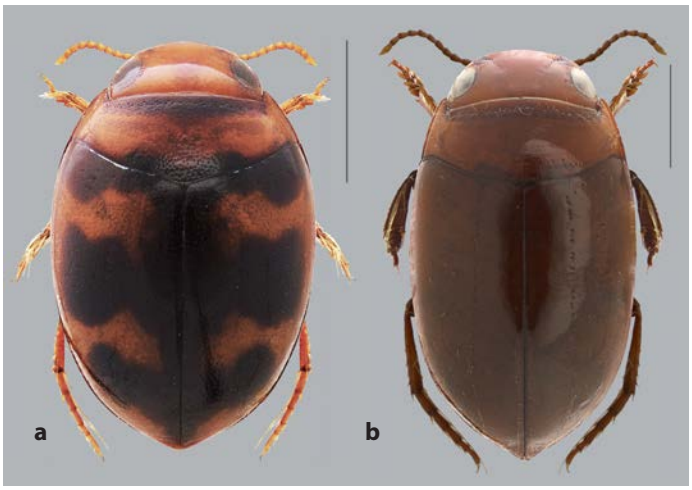


Fig. 33.4. *Hydrovatus* species. **a**, *H. cardoni*. **b**, *H. parallelipennis*. Scales = 1.0mm.

but little has been published about this. They regularly come to lights. Males of many species have what appears to be a stridulatory device formed at the border of the metaventrite and metacoxa (file) interfacing with movement of the metathoracic leg (Young, 1963; Larson and Pritchard, 1974; Biström, 1996a). In some species the males have modified antenna with variously expanded antennomeres. Larvae have been described by Spangler (1962b), Michat (2006b), and briefly (along with the egg stage) by Williams (1936).

Distribution. Species are found throughout much of the world (Map 33.1) but are most diverse in lower latitudes. There are relatively few species in the Neotropical region as compared with the Afrotropical and Oriental regions. The Nearctic region south into Central America has more species than the Neotropical.

Genus *Queda* Sharp, 1882

Body Length. 2.5–6.2mm.

Diagnosis. *Queda* are distinguished from *Hydrovatus* by the more shallow lateral excision of the posterior margin of the metacoxa (Fig. 33.1a), and the apex of the body is not acuminate (Fig. 33.5). The female genitalia differ between the two groups as well. In *Hydrovatus* the gonocoxae are together fused into a knife-like structure with elongate lateral extensions at the base (Fig. 33.3a). In *Queda*, the gonocoxae are separated and the apices are distinctly trilobed (Fig. 33.3b). Both *Q. compressa* Sharp and *Q. youngi* Biström have males with the antennomeres III–V expanded, more broadly so in *Q. youngi* (Fig. 33.5). *Queda youngi* also has males with the metatarsus dramatically modified. Metatarsomere IV is asymmetrically expanded and bilobed with clusters of stiff, curved setae (Figs. 33.1a,5).

Fig. 33.5. *Queda youngi*. Scale = 1.0mm.

Classification. The members of the group have received relatively little scientific treatment, but the relationship with *Hydrovatus* is not in doubt (Miller and Bergsten, 2014a).

Diversity. *Queda* includes only three known species, which were revised by Biström (1990). Compared with its sister group *Hydrovatus*, *Queda* are rare and poorly represented by species.

Natural History. Little is known of the natural history of *Queda*. Specimens have been collected at lights at night and in lowland tropical marshes. They are usually collected sporadically and in small series.

Distribution. The three species of *Queda* occur from southern Brazil north to Venezuela and Panama (Map 33.2).

Map 33.2. Distribution of *Queda*.

34. Tribe Pachydrini

Body Length. 3.7–6.7mm.

Diagnosis. Pachydrini are Hydroporinae with: (1) the elytral epipleuron with an oblique carina at the humeral angle (Fig. 34.1a); (2) the metacoxal lobes absent and the metacoxae medially at the same level as the abdominal sterna (Fig. 34.1a); (3) the apex of the prosternal process very broad, laterally unmargined, and broadly in contact with the metaventrite (Fig. 34.1a); (4) the metasternal wing broad medially (Fig. 34.1a); (5) the anterior metatarsal claw shorter than the posterior (Fig. 34.1c); and (6) the female genitalia with an exceptionally large bursa, long, slender fertilization duct and small, but distinctive, laterotergites (Fig. 34.1b). Members of this group also have the metacoxae fused with the abdomen (shared with Bidessini and *Desmopachria* of the Hyphydrini) and the ventrolateral carina of the elytron thick and undulating among a few other more obscure characters (see Biström *et al.*, 1997b).

Classification. This has been something of a problematic group. Originally, *Pachydrus*, *Heterhydrus,* and *Desmopachria* were placed together in Bidessini given the common fusion of the metacoxae and abdomen (Sharp, 1882). They were later placed in Hyphydrini (e.g., Zimmermann, 1920). Most recently, Biström *et al.* (1997b) placed *Pachydrus* and *Heterhydrus*, which are very similar, into their own tribe, Pachydrini, a concept suggested by Young (1980). This was disputed by Miller (2001c), who placed them back into Hyphydrini. More recent molecular analyses (e.g., Ribera *et al.*, 2002b; 2008) have indicated the genera are, indeed, not related to hyphydrines. Miller and Bergsten (2014a) also found convincing evidence that *Pachydrus* is not related to hyphydrines. *Pachydrus* and *Heterhydrus* are therefore recognized here in their own tribe following Biström *et al.* (1997b). Their relationships with other Hydroporinae are unclear, however.

Diversity. The tribe includes two genera, *Pachydrus* and *Heterhydrus.*

Natural History. Members of *Pachydrus* and *Heterhydrus* are very similar, and they occur primarily in lowland marshes and pools with considerable vegetation. They often come to lights.

Distribution. Members of Pachydrini are Afrotropical (*Heterhydrus*) and Neotropical and extreme southern Nearctic (*Pachydrus*).

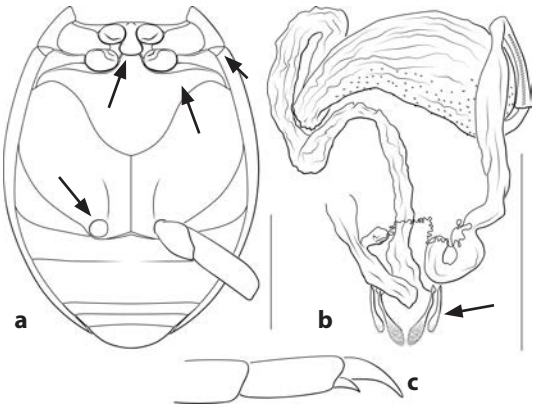


Fig. 34.1. Pachydrini features. **a**, *Pachydrus obesus*, ventral surface. **b**, *P. obesus*, female reproductive tract. **c**, *Heterhydrus senegalensis* metatarsal claws. Scales = 1.0mm

Key to the Genera of Pachydrini

1 Labrum not obscured by anterior clypeal margin in anterior perspective (Fig. 34.2a); Afrotropical (Map 34.1) . . . *Heterhydrus*, 199

1′ Labrum partly obscured by anterior clypeal margin, but anterior labral margin visible (Fig. 34.2b); southeastern Nearctic and Neotropical (Map 34.2) . . . . . *Pachydrus*, 200

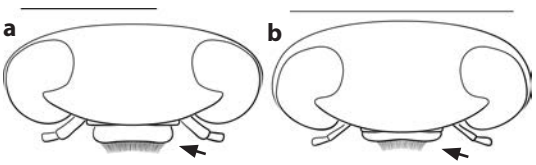


Fig. 34.2. Pachydrini heads, anterior aspect. **a**, *Heterhydrus agaboides.* **b**, *Pachydrus obesus.*

Genus *Heterhydrus* Fairmaire, 1869

Body Length. 5.0–6.7mm.

Diagnosis. From *Pachydrus*, *Heterhydrus* differs in having the labrum somewhat more visible below the clypeal margin (Fig. 34.2a). These two genera are extremely similar, and the labrum character is very subtle and unconvincing. Specimens are large, robust, and typically concolorous (Fig. 34.3).

Fig. 34.3. *Heterhydrus agaboides*. Scale = 1.0mm.

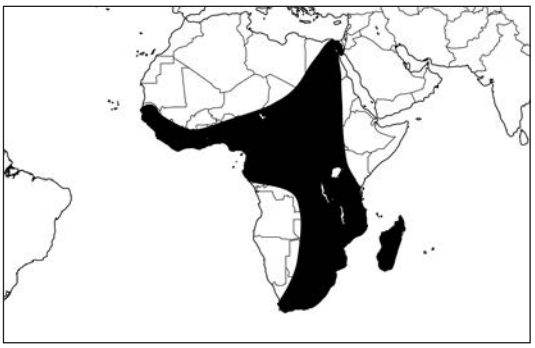
Fig. 34.4. *Pachydrus* sp. Scale = 1.0mm.

Classification. This relatively poorly known genus has so far never been included in a phylogenetic analysis with molecular data.

Diversity. There are five species assigned to *Heterhydrus* that were revised by Wewalka (1980).

Natural History. Species in this group are found in lentic habitats with dense vegetation. They come to lights but are not particularly common.

Distribution. *Heterhydrus* are known from central Africa and one species, *H. agaboides* Fairmaire, from Madagascar. The range of *H. senegalensis* (Laporte), extends north to Sinai (Map 34.1).



Map 34.1. Distribution of *Heterhydrus*.

Genus *Pachydrus* Sharp, 1882

Body Length. 3.7–6.0mm.

Diagnosis. This genus is very similar to *Heterhydrus* and differs primarily in smaller size and the labrum more distinctly concealed below the anterior portion of the clypeus (Fig. 34.2b), but this is very subtle. Specimens are nearly spherical and robust and dorsally yellowish to reddish, sometimes with vague maculae on the elytra (Fig. 34.4).

Classification. A single long-branched representative of the genus was included in the analysis by Miller and Bergsten (2014a) but was difficult to place among hydroporines with good support (*Heterhydrus* not included). Ribera *et al.* (2008) found it closest to Bidessini (again without *Heterhydrus* in the data set).

Diversity. There are currently nine species recognized in *Pachydrus*, but it has not been comprehensively revised since Sharp's (1882) monograph, and species are difficult to identify.

Natural History. *Pachydrus* can be extremely common and abundant in lowland marshes with dense vegetation and at lights. Larvae have been described by Spangler and Folkerts (1973), Crespo (1993), and Alarie and Menga (2006).

Distribution. Species in the group are found in lowland Central and South America, islands in the Caribbean, and southern Florida, USA (Map 34.2).

Map 34.2. Distribution of *Pachydrus*.

35. Tribe Hygrotini

Body Length. 2.1–7.3mm.

Diagnosis. Hygrotines are Hydroporinae with the following character states: (1) the elytral epipleuron has an oblique carina at the humeral angle (Fig. 35.1); (2) the metacoxae have broadly rounded lobes covering the bases of the metatrochanters (Fig. 35.1); (3) the metatarsal claws are equal in length (Fig. 35.2); and (4) the apices of the abdomen and elytra are not acuminate (Fig. 35.1).

Classification. In modern works, members of this tribe were placed in Hydroporini by most authors until Nilsson and Holmen (1995) recognized and diagnosed the tribe following Portevin (1929) and Houlbert (1934). There has been relatively little work done to resolve relationships among the genera within Hygrotini, though Alarie *et al.* (2001a) presented some relationships based on the few groups known from larvae. Several of the genera are not well collected and are poorly known in general, and some are poorly diagnosed over against others. For example, *Hyphoporus* and *Herophydrus* are extremely similar and may not be mutually monophyletic. One of the more problematic historical issues is the use of the name *Coelambus* as a separate genus (mainly European authors) or as a subgenus of *Hygrotus* (especially North American authors). Certain members of North American *Coelambus* (*C. masculinus* (Crotch) and *C. salinarius* Wallis) have modified anterior clypeal margins like in *Hygrotus*, but these are flattened and protruded, and are evidently not homologous with the condition in *Hygrotus* (Anderson, 1983). These species have all the other typical features of *Coelambus*. Recent analyses (e.g., Ribera *et al.*, 2008; Miller and Bergsten, 2014a) have strongly indicated that *Hygrotus s. str.* is more closely related to *Herophydrus* than to *Coelambus*. For this reason, we use the two names *Coelambus* and *Hygrotus* for separate genera here. More difficult are two other North American species, *H. laccophilinus* (LeConte) and *H. sylvanus* (Fall) (*Hygrotus* species-group II of Anderson, 1976). These species lack the modified anterior clypeal margin of *Hygrotus*, but also are different from typical *Coelambus* in being short and broad, dorsally concolorous, and in other features. It is not clear how *H. laccophilinus* and *H. sylvanus* are related to other hygrotines, but recent analyses have suggested they should be placed in their own hygrotine genus (Miller, unpublished). Until this can be investigated more thoroughly, we have retained *H. laccophilinus* and *H. sylvanus* in *Hygrotus*. Relationships of Hygrotini to other tribes are ambiguous at this time (Miller, 2001c; Ribera *et al.*, 2008; Miller and Bergsten, 2014a). Hygrotini needs substantial phylogenetic work.

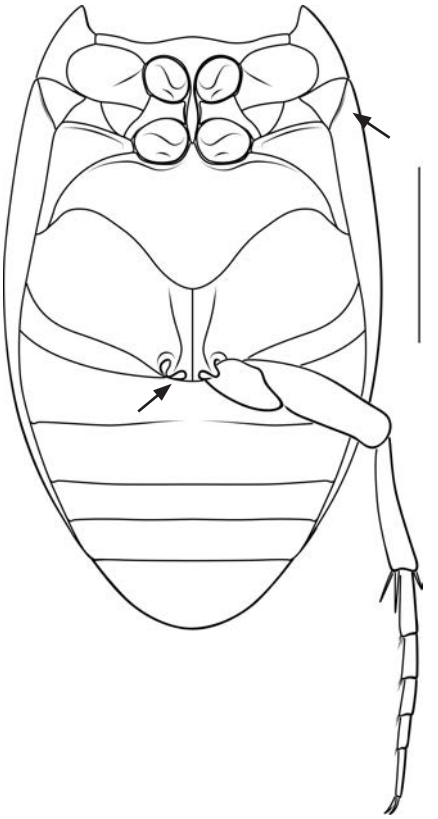


Fig. 35.1. *Coelambus patruelis* ventral surfaces. Scale = 1.0mm.

Diversity. The tribe currently includes five genera, but forthcoming revision of generic limits is likely to change this.

Natural History. This is a diverse group inhabitating many situations, but mainly in lentic habitats with emergent vegetation. There are a number of taxa, especially in *Coelambus*, that are remarkably and characteristically halotolerant.

Distribution. Hygrotines occur throughout much of the world, but members of the clade are absent from the Neotropical and Australian regions.

Fig. 35.2. *Coelambus patruelis* metatarsal claws. Scale = 0.25mm.

Key to the Genera of Hygrotini

1 Anterior clypeal margin evenly rounded, not beaded, flattened, or margined (Fig. 35.3a, except in two North American species, *C. salinarius* and *C. masculinus*) 2

1′ Anterior clypeal margin distinctly beaded, flattened, or margined (Fig. 35.3b,c), though in some taxa modification incomplete medially (Fig. 35.3c) 3

2(1) Body broadly ovate, widest slightly anterior of middle, posteriorly somewhat attenuate (Fig. 35.4a); dorsally evenly brown (Fig. 35.10b), ventrally mainly pale; Nearctic (includes two species from North America) . . . . . *Hygrotus* (in part), 205

2′ Body elongate oval, widest near middle, posteriorly rounded (Fig. 35.4b); dorsally evenly brown or black to distinctly vittate or fasciate (Fig. 35.7), ventrally mainly black; Holarctic (Map 35.1) . . . . . *Coelambus*, 203

3(1) Anterior clypeal margin narrowly and continuously beaded (Fig. 35.3b); Holarctic (Map 35.4) . . . . . *Hygrotus* (in part), 205

3′ Anterior clypeal margin broadly bordered, often discontinuous medially (Fig. 35.3c) 4

4(3) Middle antennomeres of males (and females to a lesser degree) broadly expanded (Fig. 35.5a); Madagascar (Map 35.2) . . . . . *Heroceras*, 204

4′ Middle antennomeres not expanded (Fig. 35.5b) 5

5(4) Male median lobe bilaterally asymmetrical and apically pointed (Fig. 35.6a); Southeast Asia, the Middle East, and northern Africa (Map 35.5) . . . . . *Hyphoporus*, 206

5′ Male median lobe bilaterally symmetrical and apically rounded (Fig. 35.6b); Africa, southern Palearctic to Southeast Asia (Map 35.3) . . . . . *Herophydrus*, 204

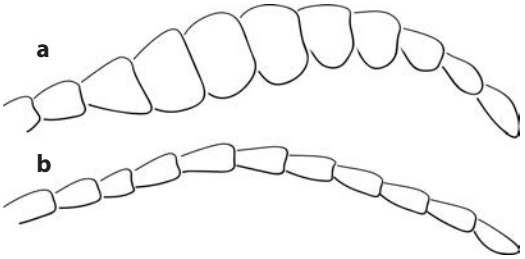


Fig. 35.5. Hygrotini right antennae. **a**, *Heroceras descarpentriesi*. **b**, *Herophydrus inquinatus*.

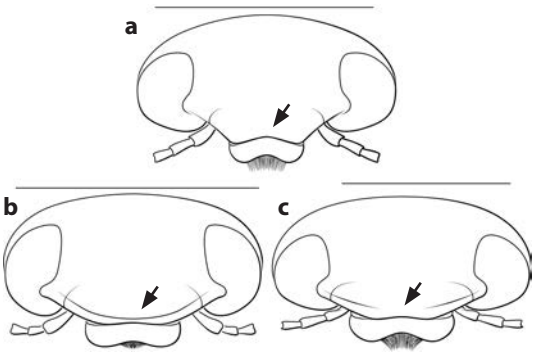


Fig. 35.3. Hygrotini heads, anterior aspect. **a**, *Coelambus patruelis*. **b**, *Hygrotus sayi*. **c**, *Herophydrus inquinatus*. Scales = 1.0mm.

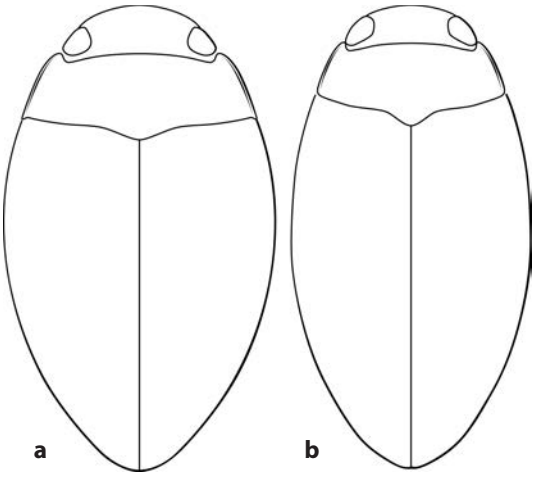


Fig. 35.4. Hygrotini habitus. **a**, *Hygrotus laccophilinus*. **b**, *Coelambus nubilus*.

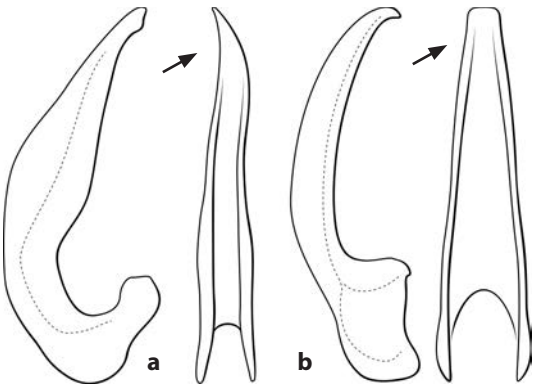


Fig. 35.6. Hygrotini male genitalia, right lateral and ventral aspects. **a**, *Hyphoporus aper*. **b**, *Herophydrus muticus*.

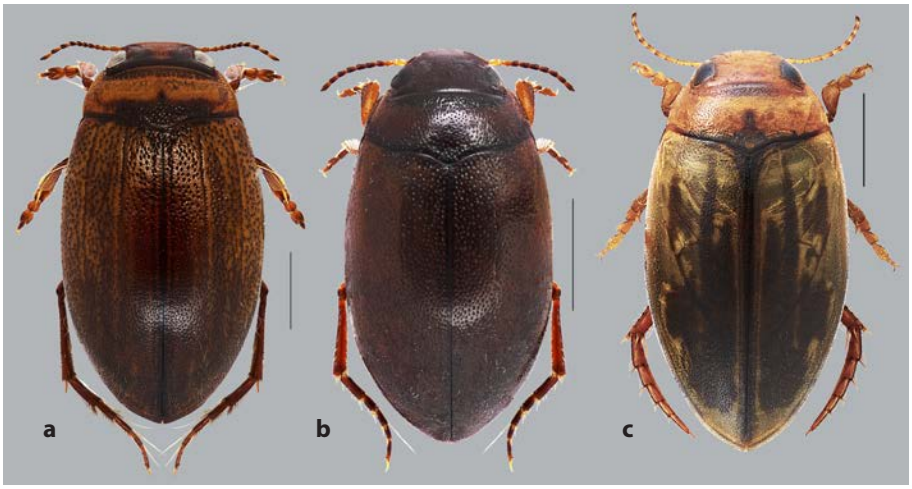


Fig. 35.7 *Coelambus* species. **a**, *C. impressopunctatus*. **b**, *C. nigrescens*. **c**, *C. nubilus*. Scale = 1.0mm.

Genus *Coelambus* Thomson, 1860

Body Length. 2.1–5.8mm.

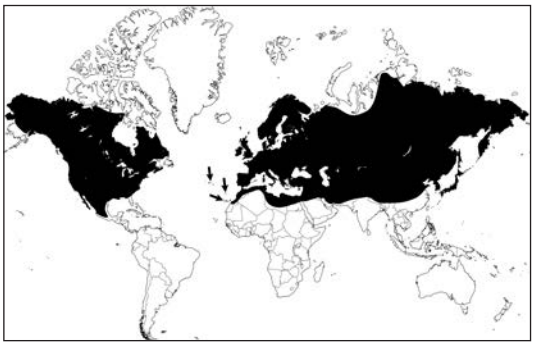
Diagnosis. Among Hygrotini, members of *Coelambus* lack modifications to the anterior clypeal margin (Fig. 35.3a) except in two Nearctic species, *C. salinarius* and *C. masculinus*, which have these margins distinctly flattened. These two species are elongate, dorsally longitudinally vittate, have similar female genitalia, and other features making them very similar to other *Coelambus*. Many members are elongate oval with longitudinal vittae (Fig. 35.7a,c), though some are brown or otherwise concolorous (Fig. 35.7b). Most have the ventral surface black.

Classification. This group has been classified as either a genus (e.g., Thomson, 1860) or as a subgenus of *Hygrotus* (e.g., F. Balfour-Browne, 1934b), with the former scheme most generally used by European authors and the latter by North American investigators. Placement as a subgenus was largely because of the challenges of character combinations in North American species, including *C. salinarius*, *C. masculinus*, *H. laccophilinus,* and *H. sylvanus*. The first two species have flattened and extended anterior clypeal margins but are otherwise very similar to other *Coelambus*. The other two species are here placed in *Hygrotus* (see below).

Diversity. There are currently 60 species in *Coelambus*. North American species can be identified using papers by Anderson (1971; 1976; 1983) and Larson *et al.* (2000). Palearctic species can be identified using Zimmermann (1930), Zaitzev (1953), and Nilsson and Holmen (1995).

Natural History. *Coelambus* are typically found in lentic habitats, including lakes, ponds, ephemeral pools, and pools in stream courses. Several species are particularly characteristic of saline waters (Rawson and Moore, 1944; Larson, 1975; Tones, 1978; Anderson, 1983; Lancaster and Scudder, 1987; Timms and Hammer, 1988; Larson *et al.*, 2000; Minakawa *et al.*, 2001). *Coelambus salinarius* can withstand an exceptional range of salt concentrations, from 12 to 71gL^{-1} (Timms and Hammer, 1988). Larvae of many species were described by Cuppen and Nilsson (1984), Galewski (1987a), Alarie *et al.* (1990b), and Barman (1999). Aspects of their biology were investigated by Cuppen (1983). Some species have rather narrow ecological ranges and tolerances (Leech, 1966; Mead, 1993). *Coelambus salinarius* is the only known diving beetle that can traverse the surface film and fly directly from the water surface (Miller, 2013a).

Distribution. This is a Holarctic taxon with members across North America, Europe, and Asia south into Mexico in the New World and across northern Africa in the Old World (Map 35.1).



Map 35.1. Distribution of *Coelambus*.

Fig. 35.8. *Heroceras descarpentriesi*. Scale = 1.0mm.

Genus *Heroceras* Guignot, 1949

Body Length. 3.3–3.5mm.

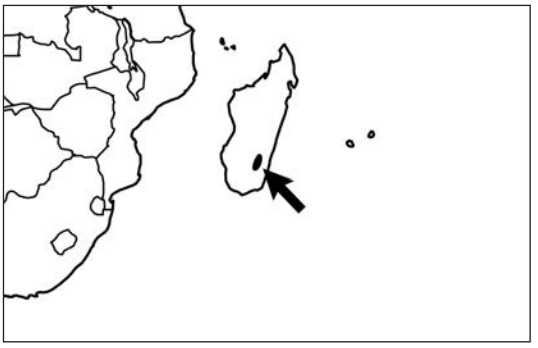
Diagnosis. *Heroceras* are similar to *Hyphoporus* and *Herophydrus* in having the anterior clypeal margin broadly bordered. *Heroceras* are unique in having the middle antennomeres broadly laterally expanded in males (Fig. 35.8). Females also have expanded antennomeres, but not as dramatically as in males.

Classification. This genus is similar to *Herophydrus* and the Southeast Asian genus *Hyphoporus*, and is probably related to them. Biström and Nilsson (2002), perhaps unsurprisingly, found *Heroceras* nested within *Herophydrus*.

Diversity. The genus contains a single species, *H. descarpentriesi* (Peschet), which was originally described in *Herophydrus* (Peschet, 1923).

Natural History. Little is known of the biology of the single species. They are very rare and have been found in mountainous areas of southern Madagascar.

Distribution. *Heroceras* are known only from the mountains of southeastern Madagascar (Map 35.2).



Map 35.2. Distribution of *Heroceras*.

Genus *Herophydrus* Sharp, 1880

Body Length. 2.9–7.4mm.

Diagnosis. This genus is very similar to *Hyphoporus* since both have the anterior clypeal margin broadly bordered, but generally (not always) with the border discontinuous medially (Fig. 35.3c) and the male antennomeres not broadly expanded (Fig. 35.9). Both are relatively globular. Historically, these two genera were differentiated based on the punctation on the head (e.g., Pederzani, 1995). *Herophydrus* was regarded as having the clypeus impunctate and *Hyphoporus* punctate. This difference does not seem to be reliable, unfortunately. The best diagnostic difference between the genera appears to be the male median lobe, which is bilaterally symmetrical and (in most species) apically more rounded or broadly truncate in *Herophydrus* (Fig. 35.6b) and bilaterally asymmetrical and (in most species) pointed in *Hyphoporus* (Fig. 35.6a). *Herophydrus* are diverse and variable with many species concolorous and others fasciate or maculate (Fig. 35.9).

Classification. *Herophydrus* were originally described in *Hydroporus* or *Hyphydrus* before Sharp (1882) placed them in a new genus along with several new species. Relationships of the group to other hygrotines are not well established, though *Herophydrus* has been resolved near *Hygrotus* (Ribera *et al.*, 2008; Miller and Bergsten, 2014a), and species

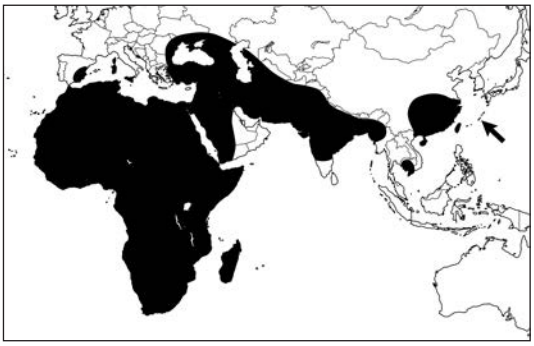
Fig. 35.9. *Herophydrus inquinatus*. Scale = 1.0mm.

are extremely similar to *Hyphoporus*. Relationships with this genus, in particular, need investigation.

Diversity. The genus contains 44 species and was revised by Biström and Nilsson (2002).

Natural History. Specimens have been collected from ponds, streams, swamps, ditches, temporary pools, etc. Biström and Nilsson (2002) reviewed the numerous biology data from the literature and labels. Larvae were described by Alarie *et al.* (2001a) and Bertrand (1963).

Distribution. *Herophydrus* are primarily Afrotropical, including Madagascar, with species also in southern Europe and the Middle East through Kashmir to Southeast Asia and China (Map 35.3).

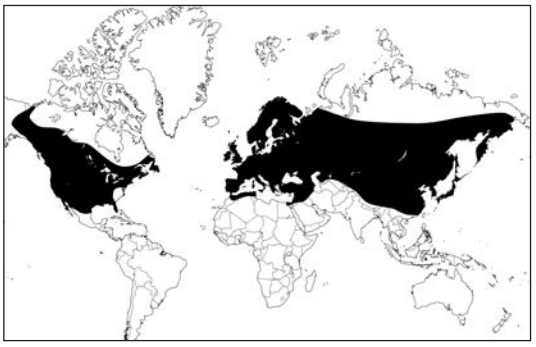


Map 35.3. Distribution of *Herophydrus*.

Genus *Hygrotus* Stephens, 1828

Body Length. 2.2–3.6mm.

Diagnosis. Within the tribe, *Hygrotus* are characterized by a narrow bead entirely across the anterior clypeal margin (Fig. 35.3b). These beetles are robust and globular. (Fig. 35.10). Many species are dorsally attractively marked with fasciae or maculae (Fig. 35.10a). A few species have males with the last abdominal sternite modified with spines or other structures.



Map 35.4. Distribution of *Hygrotus*.

Classification. *Hygrotus* has been grouped historically with *Coelambus* (with the latter a subgenus of *Hygrotus*), but the two are not as closely related as *Hygrotus* is to *Herophydrus* (Ribera *et al.*, 2008; Miller and Bergsten, 2014a) (see above).

Diversity. The group has 13 species. Nearctic species were revised by Anderson (1971) and Larson *et al.* (2000). Palearctic species are identifiable using Nilsson and Holmen (1995), Zimmermann (1930), Franciscolo (1979a), and Zaitzev (1953).

Natural History. These species can be found in many habitats but are usually in lentic situations with some vegetation. Some aspects of their natural history were discussed by Cuppen (1983), who described species preferences for different habitats. Larvae were described by Cuppen and Nilsson (1984),

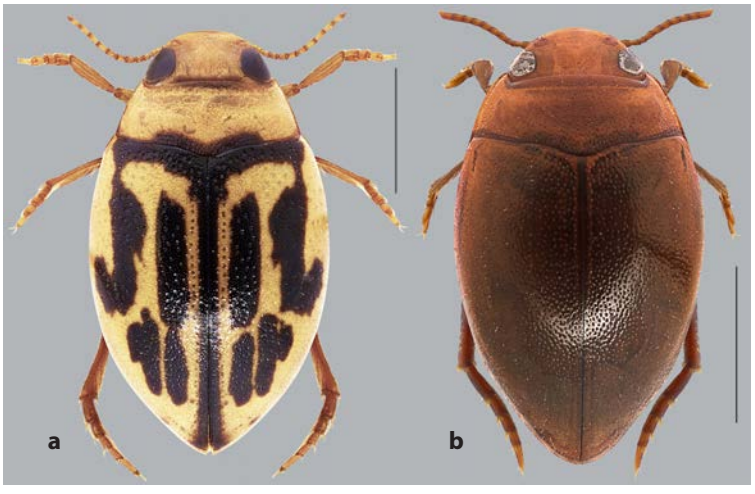


Fig. 35.10. *Hygrotus* species. **a**, *H. versicolor*. **b**, *H. laccophilinus*. Scales = 1.0mm.

Spangler and Gillespie (1973), Galewski (1987a), and Alarie *et al.* (1990b).

Distribution. This is a Holarctic group with species throughout North America south into Mexico, Europe, northern Africa, and across Asia (Map 35.4).

Genus *Hyphoporus* Sharp, 1880

Body Length. 3.5–5.6mm.

Diagnosis. This genus is very similar to *Herophydrus* since both have the anterior clypeal margin broadly bordered, but generally with the border discontinuous medially (Fig. 35.3c) and the male antennomeres not broadly expanded (Fig. 35.11). *Hyphoporus* differs from *Herophydrus* in the bilaterally asymmetrical shape of the male median lobe (Fig. 35.6a). See above under *Herophydrus* for additional diagnostics. Members of *Hyphoporus* are variable, but often dorsally maculate or fasciate (Fig. 35.11).

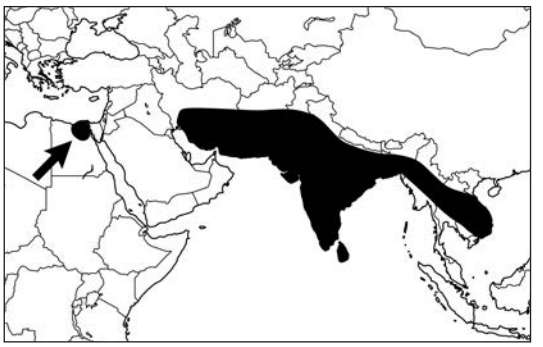
Classification. This group is very similar to *Hyphoporus*, and their monophyly with respect to each other has not been well investigated.

Diversity. There are 19 species of *Hyphoporus* currently recognized. The highest diversity is in India, where they were revised by Vazirani (1969), but other species have not been treated.

Natural History. Specimens are often found in lentic and slow lotic situations with considerable vegetation. They occur mainly in lowlands and not in mountainous areas (Vazirani, 1969). Feeding habits were investigated by Sen and Ehsan (1988). Bisht and Das (1979b) investigated their sex ratio and dimorphism.

Distribution. These species are found from Iran through India to Southeast Asia with one species in Egypt (Map 35.5). Ghosh and Nilsson (2012) provide the distributions in India, where their diversity is highest.

Fig. 35.11. *Hyphoporus aper*. Scale = 1.0mm.



Map 35.5. Distribution of *Hyphoporus*.

36. Tribe Hyphydrini

Body Length. 0.96–6.8mm.

Diagnosis. Hyphydrini are Hydroporinae that have: (1) the elytral epipleuron with an oblique carina at the humeral angle (Fig. 36.1a); (2) the metacoxal lobes absent (Fig. 36.1a) or extremely small and subtriangular (Fig. 36.1b) and the metacoxae medially at the same level as the abdominal sterna (Fig. 36.1a); (3) the apex of the prosternal process narrow and pointed (Fig. 36.1a); (4) the metasternal wing narrow medially (Fig. 36.1a); and (5) the anterior metatarsal claw shorter than the posterior (Fig. 36.1c). The difference in length between the metatarsal claws is not as pronounced in some *Allopachria* and *Microdytes*. Also, the metacoxa is fused with the first visible abdominal ventrite in *Desmopachria*, *Microdytes*, and *Allopachria*, but not in other taxa (convergent with Pachydrini and many Bidessini).

Classification. Hyphydrini genera have been variously classified historically. Sharp (1882) thought *Pachydrus*, *Heterhydrus*, *Desmopachria,* and Bidessini may be related based on fusion of the metacoxae with the first abdominal ventrite. Also, *Microdytes* was placed in Hydrovatini by Nilsson *et al*. (1989) and later placed back into Hyphydrini by Biström (1996a). However, most members of the group have been usually placed as they are now (see Biström *et al.,* 1997b). A significant exception includes *Pachydrus* and *Heterhydrus*, two very similar genera, that were placed in a separate tribe, Pachydrini, by Biström *et al.* (1997). Miller (2001a) and Miller *et al.* (2006) found that these genera were resolved with Hyphydrini based on evidence from morphology. Ribera *et al.* (2008) found them, again, phylogenetically distant from Hyphydrini and sister to Bidessini, similar to Ribera and Balke (2007), and they resurrected the tribe. Based on larval morphology, Michat *et al.* (2008), somewhat tentatively, concluded that Pachydrini is sister to Hydrovatini. Miller and Bergsten (2014a) also found *Pachydrus* sister to Hydrovatini, and here we recognize separate tribes Hyphydrini and Pachydrini, following Biström *et al.* (1997b). Ribera and Balke (2007) investigated the phylogeny within Hyphydrini. They concluded that there are four well-supported clades among the group: (1) *Hyphydrus*, (2) the five unusual South African genera (*Andex*, *Coelhydrus*, *Primospes*, *Darwinhydrus*, *Hydropeplus*) plus the Madagascan *Hovahydrus*, (3) *Desmopachria*, and (4) *Microdytes* + *Allopachria*, with a few other genera not included in the analysis.

Diversity. The tribe includes 14 genera.

Natural History. Hyphydrines occur in a wide range of habitat types, but many species are in heavily vegetated lakes and others are in streams of various sizes. Some are only in seeps and springs. At least one species of *Microdytes* and the single species in *Dimitshydrus* are subterranean (Uéno, 1996; Wewalka *et al.,* 2007).

Distribution. This group is circumtropical with a few species (*Desmopachria*) extending north into eastern Canada and a few others (*Hyphydrus*) extending north into northern Europe, Hokkaido, and far east Russia. Several unusual genera (*Andex*, *Coelhydrus*, *Primospes*, *Darwinhydrus*, *Hydropeplus*) are endemic to extreme southern Africa.

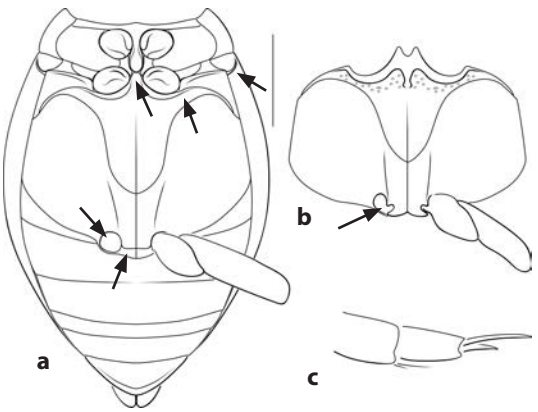


Fig. 36.1. Hyphydrini features. **a**, *Hyphydrus* sp. ventral surfaces. **b**, *Allopachria quadripustulata* thoracic sterna. **c**, *Microdytes sabitae* metatarsal claws. Scale = 1.0mm (a).

Key to the Epigean Genera of Hyphydrini

One genus in Hyphydrini, *Dimitshydrus*, and one species of *Microdytes* are subterranean. Like in other groups, these taxa have features common to troglodytic diving beetles, including flighlessness, anopthalmy, depigmentation, etc. (e.g., Fig. 3.51) and are keyed separately in the key to subterranean taxa (page 45).

1 Apex of prosternal process not reaching metaventrite (Fig. 36.2); South Africa (Map 36.3) . . . . . *Andex*, 210

1' Apex of prosternal process reaching metaventrite (Fig. 36.1). 2

2(1) Pronotum with posterolateral angle extended posteriorly (Fig. 36.3a) and length < 3.3mm; Nearctic and Neotropical (Map 36.7) . . . . . *Desmopachria*, 213

2' Pronotum with posterolateral angle not extended posteriorly (Fig. 36.3b), or extended but length > 3.2mm (Fig. 36.9a) 3

3(2) Elytron with longitudinal carina (Fig. 36.16); South Africa (Map 36.6) . *Darwinhydrus*, 212

3' Elytron without longitudinal carina. 4

4(3) Base of metatrochanter obscured by small, triangular lobe of metacoxal process (Fig. 36.4a). 5

4' Base of metatrochanter completely exposed, metacoxa without lobe (Fig. 36.4b). 7

5(4) Prosternal process with small, medial prominence or denticle (Fig. 36.5a); India and Southeast Asia (Map 36.13) . *Microdytes*, 217

5' Prosternal process without medial prominence (Fig. 36.5b) 6

6(5) Body short and globular (Fig. 36.12); punctures on metaventrite coarse, including on metasternal wings (Fig. 36.6a); mesocoxae broadly separated and anterior process of metaventrite bifurcated (Fig. 36.6a); Southeast Asia (Map 36.2). . . . . *Allopachria*, 210

6' Body extremely elongate and strongly flattened (Fig. 36.14); punctures on metaventrite only present proximally, reduced and indistinct on metasternal wings (Fig. 36.6b); mesocoxae closely approximated and anterior process of metaventrite not bifurcated (Fig. 36.6b); Southeast Asia (Map 36.4) . . . . . *Anginopachria*, 211

7(4) Clypeus with anterior margin beaded or flattened and upturned (Fig. 36.8a,b); if clypeal bead indistinct, then anterior metatibial spur serrate (Fig. 36.7a). 8

7' Clypeus with anterior margin unmodified, evenly rounded (Fig. 36.8c). 9

8(7) Clypeus with distinct broad marginal bead (Fig. 36.8a), if bead indistinct then anterior metatibial spur serrate (Fig. 36.7a); much of Old World (Map 36.12) . . . . *Hyphydrus*, 216

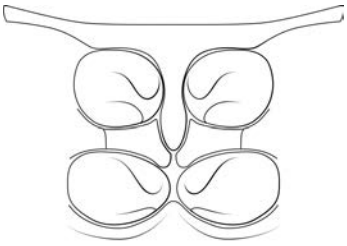


Fig. 36.2. *Andex insignis* prosternal process.

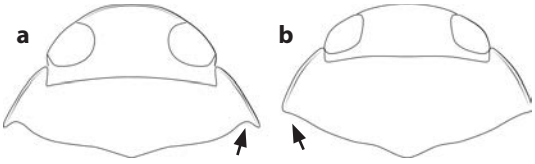


Fig. 36.3. Hyphydrini heads and pronota. **a**, *Desmopachria convexa*. **b**, *Hyphydrus signatus*.

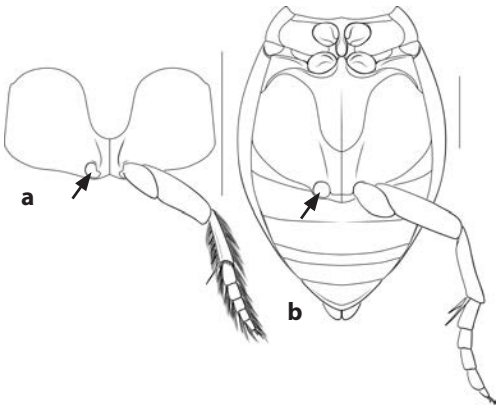


Fig. 36.4. Hyphydrini ventral surfaces. **a**, *Microdytes sabitae*. **b**, *Hyphydrus ovatus*. Scales = 1.0mm.

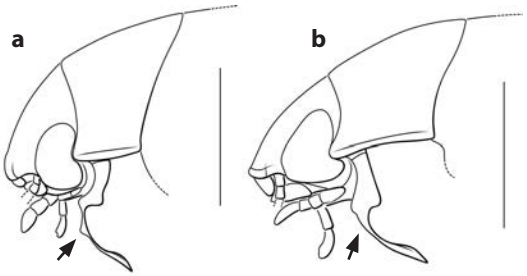


Fig. 36.5. Hyphydrini lateral aspect. **a**, *Microdytes sabitae*. **b**, *Allopachria quadripustulata*. Scales = 0.5mm.

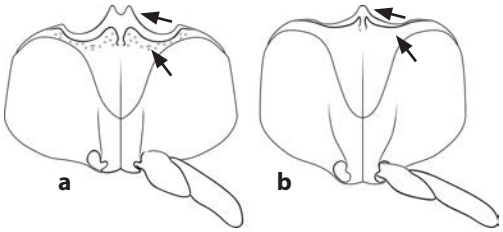


Fig. 36.6. Hyphydrini metaventrite and metacoxae. **a**, *Allopachria quadripustulata*. **b**, *Anginopachria ullrichi*.

8' Clypeus with anterior margin flattened and distinctly upturned (Fig. 36.8b), metatibial spurs not serrate (as in Fig. 36.7b); Madagascar (Map 36.9) . . . . . *Hovahydrus*, 214

9(7) Larger, total length 3.8–5.2mm; body shape elongate (Figs. 36.15,21,25); South Africa . 10
9' Smaller, total length 1.9–3.0mm; body shape globular (Figs. 36.11,22); Southeast Asia . . 12

10(9) With posterolateral angles of pronotum strongly produced posteriorly and sharply acute (Fig. 36.9a); South Africa (Map 36.14) . . . . . *Primospes*, 218
10' With posterolateral angles of pronotum not produced, not acute (Fig. 36.9b,c) 11

11(10) Lateral body outline continous between pronotum and elytron (Fig. 36.9b); South Africa (Map 36.5) . . . . . *Coelhydrus*, 212
11' Lateral body outline distinctly discontinuous between pronotum and elytron (Fig. 36.9c); South Africa (Map 36.10) . . *Hydropeplus*, 215

Fig. 36.9. Hyphydrini heads and pronota. **a**, *Primospes suturalis*. **b**, *Coelhydrus brevicollis*. **c**, *Hydropeplus trimaculatus*.

12(9) Apex of median lobe bifurcate (Fig. 36.10a); Southeast Asia (Map 36.11). *Hyphovatus*, 216
12' Apex of median lobe not bifurcate (Fig. 36.10b); Southeast Asia (Map 36.1) . . . . . *Agnoshydrus*, 209

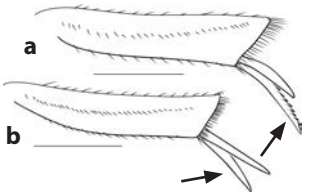


Fig. 36.7. Hyphydrini metatibiae. **a**, *Hyphydrus ovatus*. **b**, *Hydropeplus trimaculatus*. Scales = 0.5mm.

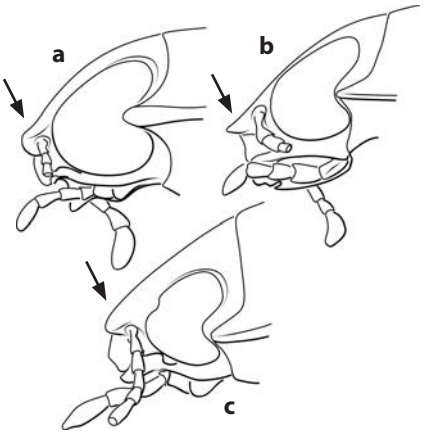


Fig. 36.8. Hyphydrini heads, lateral aspect. **a**, *Hyphydrus renardi*. **b**, *Hovahydrus* sp. **c**, *Hydropeplus trimaculatus*.

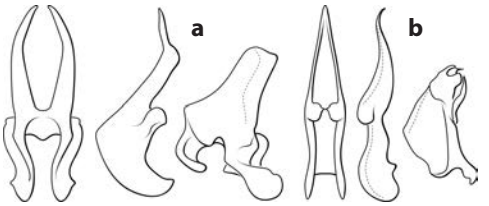


Fig. 36.10. Hyphydrini male genitalia, median lobe ventral aspect, median lobe, right lateral aspect, lateral lobe right lateral aspect. **a**, *Hyphovatus dismorphus*. **b**, *Agnoshydrus schillhammeri*.

Fig. 36.11. *Agnoshydrus* sp. Scale = 1.0mm.

Genus *Agnoshydrus* Biström, Nilsson, and Wewalka, 1997

Body Length. 1.9–2.7mm.

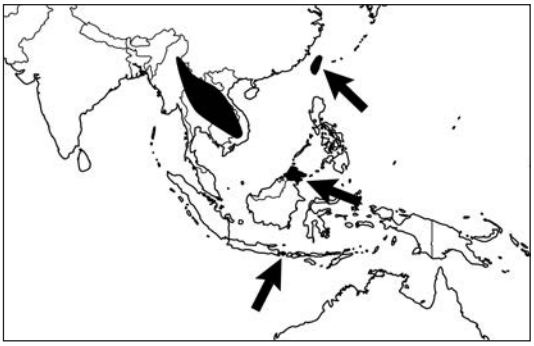
Diagnosis. *Agnoshydrus* are distinguishable from other hyphydrines by: (1) the base of the metatrochanter completely exposed, not partially covered by a small lobe of the metacoxa (as in Fig. 36.4b); (2) the anterior margin of the clypeus not beaded (as in Fig. 36.8c); (3) the median lobe of the aedeagus not apically bifurcate (Fig. 36.10b); and (4) fine, dense, evenly distributed punctation covering the dorsal surface (Fig. 36.11). Species in this group are small and globular (Fig. 36.11).

Classification. Nothing is known of *Agnoshydrus* relationships with other hyphydrines.

Diversity. There are eight poorly known *Agnoshydrus* species which were treated by Wewalka (1999).

Natural History. Most of the known specimens in this group have been collected at lights.

Distribution. *Agnoshydrus* are known only from Southeast Asia, including Taiwan, Sabah, and Bali (Map 36.1).



Map 36.1. Distribution of *Agnoshydrus*.

Genus *Allopachria* Zimmermann, 1924

Body Length. 1.4–3.1mm.

Diagnosis. This genus can be distinguished from other hyphydrine genera by the following: (1) the posterolateral angles of the pronotum are not acute nor extended posteriorly (as in Fig. 36.3b); (2) the elytra are not longitudinally keeled (Fig. 36.12); (3) the base of the metatrochanter is partially concealed by a small, triangular lobe on the metacoxal process (as in Fig. 36.4a); and (4) the prosternal process does not have a tubercle or process at the base (Fig. 36.5b). Species in this genus are very similar to *Microdytes*, but that genus has a distinct tubercle at the base of the prosternum (Fig. 36.5a). *Allopachria* are small to extremely small and often maculate (Fig. 36.12). Some species have antennomeres III and/or IV modified and asymmetrically expanded in various ways (Fig. 36.12), and some have the male protibiae or protarsomeres modified (Wewalka, 2000).

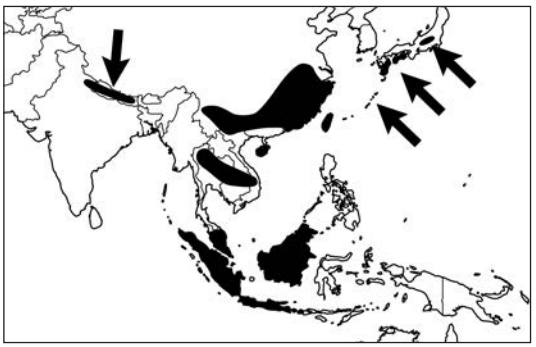
Fig. 36.12. *Allopachria beeri*. Scale = 1.0mm.

Classification. Little is known of relationships of *Allopachria*, though it was nested within *Microdytes* in the analysis by Ribera and Balke (2007).

Diversity. There are currently 47 species of *Allopachria*, most of which were revised by Wewalka (2000) with numerous new species described after that, especially by Wewalka (2010).

Natural History. This group is characteristic of slow streams in tropical forests (Wewalka, 2010).

Distribution. Species in this group occur from northern India and Nepal east to China and Japan and south to Indonesia (Map 36.2). The known distribution is sporadic and disjunct (Map 36.2), but probably reflects difficulty in collecting this region more than actual distributions.



Map 36.2. Distribution of *Allopachria*.

Genus *Andex* Sharp, 1882

Body Length. 5.5–6.0mm.

Diagnosis. This genus is one of relatively few diving beetle groups (and the only genus in Hyphydrini) in which the prosternal process does not reach the metaventrite and is instead separated from it by the contiguous mesocoxae (Fig. 36.2). Specimens are moderately large for Hyphydrini and elongate with a strong discontinuity in curvature between the pronotum and elytra (Fig. 36.13).

Classification. *Andex* has been classified in Hyphy-

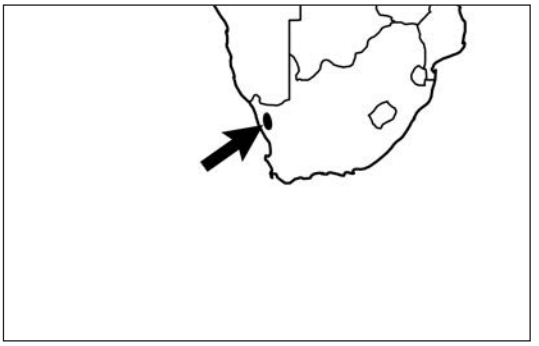
Fig. 36.13. *Andex insignis*. Scale = 1.0mm.

drini since first described. Omer-Cooper (1965a), Biström *et al*. (1997b), Toledo and Turner (2004), Challet and Turner (2006), and Ribera and Balke (2007) each briefly addressed the taxonomy of the group. Ribera and Balke (2007) found the species to be sister to *Hydropeplus*, another South African hyphydrine genus.

Diversity. There is a single species in the genus, *A. insignis* Sharp.

Natural History. *Andex insignis* has been considered a rare species (Omer-Cooper, 1965a; Toledo and Turner, 2004; Challet and Turner, 2006), but it appears to be common in the few localities in which it has been collected, which are streams in northern extensions of fynbos habitats in western South Africa (Toledo and Turner, 2004; Challet and Turner, 2006). Omer-Cooper (1965a) believed the species to be a coastal plain inhabitant, but this is not true, though specimens disperse farther into the lowlands during the wet season (Challet and Turner, 2006). Larvae were described by Alarie and Challet (2006b).

Distribution. Andex occurs only in the northwestern part of the Cape region, South Africa (Map 36.3).



Map 36.3. Distribution of *Andex*.

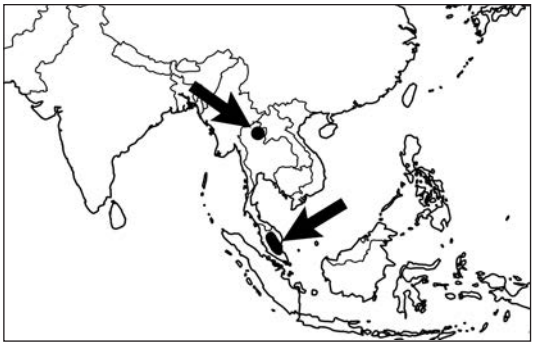
Fig. 36.14. *Anginopachria ullrichi*. Scale = 1.0mm.

Genus *Anginopachria* Wewalka, Balke, and Hendrich, 2001

Body Length. 1.4–1.8mm.

Diagnosis. This genus is characterized within the tribe by: (1) the base of the metatrochanter partially concealed by a small lobe on the metacoxal process (Fig. 36.6b); (2) no medial tubercle present on the prosternal process (as in Fig. 36.5b); and (3) the body not globular and with the mesocoxae narrowly separated (Fig. 36.14). Specimens are very small (length < 1.8mm) and are similar to *Microdytes* and *Allopachria*, but can be distinguished using the abovementioned features. *Anginopachria* are relatively flattened and elongate (Fig. 36.14). Recently discovered species of *Microdytes* from India (Miller and Wewalka, 2010) are more elongate and flattened like *Anginopachria*, but they have a medial tubercle on the prosternal process.

Classification. Nothing is known of *Anginopachria* relationships to other hyphydrines.



Map 36.4. Distribution of *Anginopachria*.

Diversity. This genus contains three species, the type species *A. ullrichi* (Balke and Hendrich), and two others, *A. prudeki* Wewalka *et al.* and *A. schoedli* Wewalka *et al.* (Wewalka *et al.,* 2005).

Natural History. Little is known about this group. Specimens have been collected at light and in a pool with a sandy substrate (Wewalka *et al.,* 2001; 2005).

Distribution. Species are known from Malaysia and Thailand (Map 36.4).

Genus *Coelhydrus* Sharp, 1882

Body Length. 3.8–4.0mm

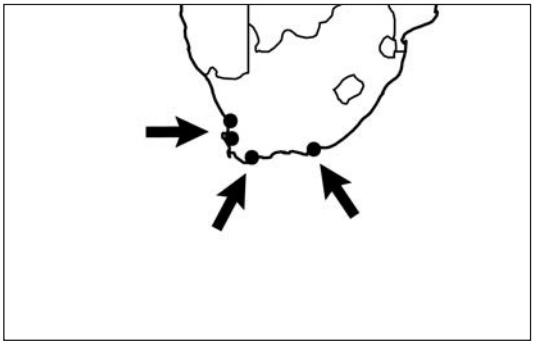
Diagnosis. *Coelhydrus* (1) do not have a modified anterior clypeal margin (as in Fig. 36.8c); (2) the apex of the prosternal process reaches the metaventrite between the mesocoxae (Fig. 36.1a); (3) the posterolateral angles of the pronotum are not acutely extended posteriorly (Fig. 36.9b); (4) the elytra do not have longitudinal carinae (Fig. 36.15); (5) the base of the metatrochanter is completely exposed, not covered by a lobe (as in Fig. 36.1a); and (6) the overall habitus is robust but elongate oval with the lateral margins approximately continuously curved between the pronotum and elytron (Figs. 36.9b,15). Specimens are medium sized for the group and relatively pale and globular (Fig. 36.15).

Classification. The genus has been classified in the tribe since first described. It belongs to a clade with the other unusual South African hyphydrines as sister to the four genera *Andex*, *Darwinhydrus*, *Primospes*, and *Hydropeplus* (Ribera and Balke, 2007; Ribera *et al.,* 2008).

Diversity. There is only a single species in the genus, *C. brevicollis* Sharp.

Natural History. *Coelhydrus brevicollis* is, historically, a very rarely collected species (Challet and Turner, 2006). Challet and Turner (2006) provided a number of details about the habitat of *C. brevicollis*. Notably, specimens occur in brackish water (Omer-Cooper, 1965a; Challet and Turner, 2006).

Distribution. *Coelhydrus brevicollis* is known only from a few localities in extreme southern South Africa (Map 36.5).



Map 36.5. Distribution of *Coelhydrus*.

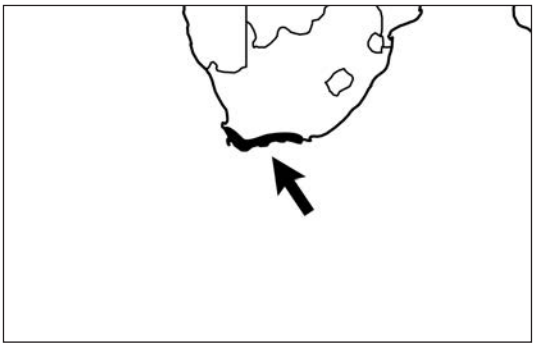
Genus *Darwinhydrus* Sharp, 1882

Body Length. 3.2–3.6mm.

Diagnosis. *Darwinhydrus* are hyphydrines with longitudinal carinae on the elytra (Fig. 36.16). They also have the anterior clypeal margin unmodified (as in Fig. 36.8c) and are relatively globular (Fig. 36.16). Specimens are medium sized for the group.

Fig. 36.15. *Coelhydrus brevicollis.* Scale = 1.0mm.

Fig. 36.16. *Darwinhydrus solidus.* Scale = 1.0mm.



Map 36.6. Distribution of *Darwinhydrus*.

Classification. The genus has been in the tribe since first described. It belongs to a clade with the other South African hyphydrines *Andex*, *Coelhydrus*, *Primospes*, and *Hydropeplus* (Ribera *et al.,* 2008).

Diversity. There is only a single species in the genus, *D. solidus* Sharp.

Natural History. *Darwinhydrus* is one of five Cape genera of Hyphydrini that are very narrowly distributed. The biology is poorly known but it has been collected from vegetated lentic pools and marshes.

Distribution. *Darwinhydrus solidus* is found only in the Cape region of South Africa (Map 36.6).

Genus *Desmopachria* Babington, 1841

Body Length. 0.96–3.3mm.

Diagnosis. *Desmopachria* are hyphydrines with the following features: (1) the apex of the prosternal process is in contact with the anterior margin of the metaventrite (a few species have males with the prosternal process apically bifid with a deep pit between the branches) (Fig. 36.18) and (2) the posterolateral margins of the pronotum are distinctly acutely angled and extended posteriorly (Fig. 36.3a). This last character is also present in the South African *Primospes*, but they are much larger (>3.0mm). *Desmopachria* are typically small to extremely small, with most <2mm in length. The largest species, *D. rex* Gustafson and Miller, is unusual at nearly 3.3mm (Gustafson and Miller, 2012). *Desmopachria* are globular and often brown to black, though many species are dorsally maculate or otherwise patterned (Fig. 36.17).

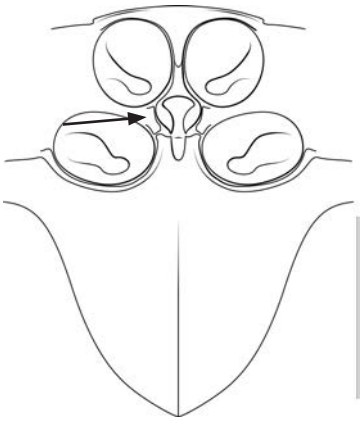


Fig. 36.18. *Desmopachria portmanni*, thoracic sterna.

Classification. This genus was placed in Bidessini by Sharp (1882) based on fusion of the metacoxae to the first visible abdominal segment but was moved into Hyphydrini by Zimmermann (1920). This large genus was nearly entirely revised in a series of papers by Young (1951; 1955; 1979a; 1980; 1981a–c; 1986a; 1989b; 1990a; b; 1993; 1995). He recognized several subgenera (Young, 1980), but Miller (2001a) synonymized them all with the nominal genus and

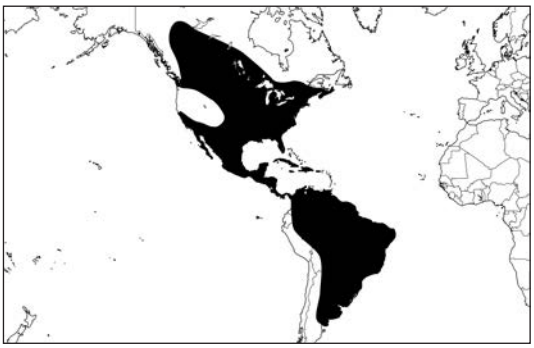
Fig. 36.17. *Desmopachria* species. **a**, *D. convexa*. **b**, *D. portmanni*. Scales = 1.0mm.

instead recognized informal species groups since at least one subgenus, *Desmopachria s. str.* (and possibly others), is not evidently monophyletic.

Diversity. This is a large group with currently 116 described species and a great many more to be described (Miller, unpublished).

Natural History. These beetles occur mostly in standing waters, especially marshes and ponds, but also in leaf-choked forest pools and phytotelmata, including bromeliad leaf axils. Some are typical of streams or desert pools with mineral substrates. Larvae have been described (Barman, 1973).

Distribution. This taxon is restricted to the New World from eastern Canada south and west to Arizona and throughout Mexico and Central and South America, mainly in the lowlands (Map 36.7).



Map 36.7. Distribution of *Desmopachria*.

Genus *Dimitshydrus* Uéno, 1996

Body Length. 1.8–2.2mm.

Diagnosis. This is one of a couple taxa in Hyphydrini that are subterranean, and specimens lack eyes and pigmentation and have other features associated with that lifestyle (Fig. 36.19). *Dimitshydrus* differ from *Microdytes trontelji* Wewalka, Ribera, and Balke, the other subterranean hyphydrine species, in being short, broadly rounded, and robust (Fig. 36.19), rather than elongate oval and dorsoventrally compressed, and having the eyes absent (Fig. 36.19), instead of reduced and V-shaped (Wewalka *et al.*, 2007). Also, the anterior clypeal margin is finely bordered in *Dimitshydrus*.

Classification. The relationship with other hyphydrines is unknown, but Uéno (1996) thought *Dimitshydrus* are most similar to *Allopachria* or, especially, *Microdytes*.

Diversity. There is one species in the genus, *D. typhlops* Uéno.

Fig. 36.19. *Dimitshydrus typhlops*. Scale = 1.0mm.

Natural History. *Dimitshydrus typhlops* are subterranean. Uéno (1996) provided a number of details about their swimming and feeding behaviors. They feed on microcrustacea and a "fluffy sediment of unknown nature" and are tolerant of a narrow range of temperatures (Uéno, 1996). The species occurs with other subterranean arthropods, including the hydradephagan beetle, *Phreatodytes mohrii* Uéno.

Distribution. The species is known only from the Sukagawa Aquifer at Uwajima-Shi, Ehimé Prefecture on the western coast of Shikoku, Japan (Map 36.8).

Map 36.8. Distribution of *Dimitshydrus*.

Genus *Hovahydrus* Biström, 1982

Body Length. 1.9–3.1mm.

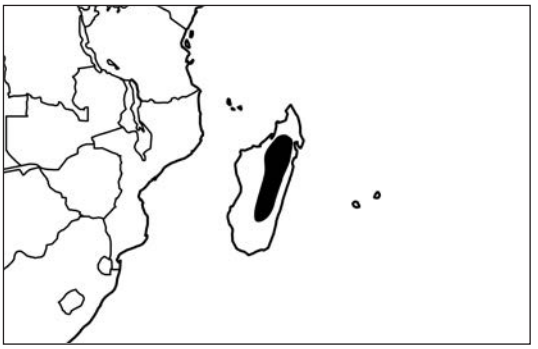
Diagnosis. This group is characterized by the following: (1) the apex of the prosternal process reaches the metaventrite (as in Fig. 36.1a); (2) the pronotum has the posterolateral angles not acutely extending

Fig. 36.20. *Hovahydrus minutissimus.* Scale = 1.0mm.

posteriorly (Fig. 36.20); (3) the elytra do not have longitudinal carinae (Fig. 36.20); (4) the metacoxae do not have lobes and the metacoxal cavities are completely exposed (as in Fig. 36.4b); (5) the anterior clypeal margin is narrowly flattened and upturned (Fig. 36.8b); (6) the apex of the median lobe is not bifurcate; and (7) the dorsal surface is smooth or, if punctate, the punctures are irregular and coarse (Fig. 36.20). This genus is similar to *Agnoshydrus* but differs by the modification of the anterior clypeal margin in *Hovahydrus* and some features associated with the male genitalia. The median lobe is variable, but not apically dorsoventrally flattened or curved as in *Agnoshydrus*, and the lateral lobe has a slender apical extension. *Hovahydrus* are similar to *Hyphydrus* but are smaller (length < 3.1mm), and *Hyphydrus* have the anterior clypeal margin broadly or indistinctly beaded (Fig. 36.8a). *Hovahydrus* are globular and often dorsally patterned or maculate (Fig. 36.20).

Classification. The genus was resolved as sister to the endemic South African genera in the analysis by Ribera and Balke (2007).

Diversity. This is a small genus with only four currently recognized species, though several new species are known (Bergsten, unpublished). They were revised by Biström (1982b).



Map 36.9. Distribution of *Hovahydrus*.

Natural History. Little is published about *Hovahydrus* natural history, but they are lotic in streams from 700m elevation and higher. They are generally rare but can occasionally be found in larger series.

Distribution. *Hovahydrus* are found only in highland regions of Madagascar (Map 36.9).

Genus *Hydropeplus* Sharp, 1882

Body Length. 4.9–5.2mm.

Diagnosis. *Hydropeplus* are hyphydrines with: (1) the anterior clypeal margin unmodified (Fig. 36.8c); (2) the body relatively large and elongate oval with the lateral outline discontinuous between the pronotum and the elytron (Fig. 36.21); (3) the elytra without longitudinal carinae (Fig. 36.21); (4) the metacoxa without a lobe obscuring the base of the metatrochanter (as in Fig. 36.1a); (5) the apex of the prosternal process extending to the metaventrite; and (6) the pronotum with the posterolateral angles obtuse, not extending posteriorly as an acute angle (Fig. 36.21).

Classification. *Hydropeplus* were resolved as sister to *Andex* in the analysis by Ribera and Balke (2007).

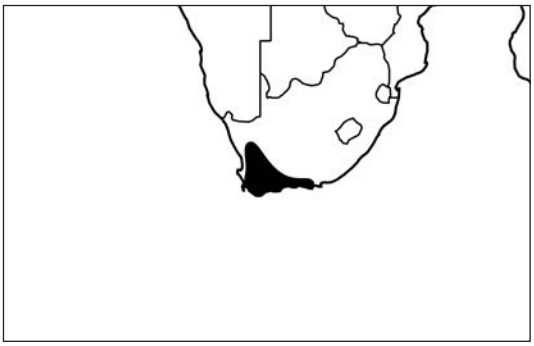
Diversity. There are currently only two similar species recognized in the genus, *H. trimaculatus* (Laporte) and *H. montanus* Omer-Cooper. The species were treated by Omer-Cooper (1965a).

Natural History. *Hydropeplus* are found on the

Fig. 36.21. *Hydropeplus trimaculatus.* Scale = 1.0mm.

coastal plain and in the mountains along the western Cape (Omer-Cooper, 1965a), in streams.

Distribution. Members of the genus are known only from the Cape region of South Africa (Map 36.10).



Map 36.10. Distribution of *Hydropeplus*.

Genus *Hyphovatus* Wewalka and Biström, 1994

Body Length. 2.6–3.0mm.

Diagnosis. This genus is similar to *Agnoshydrus* and *Hovahydrus* in being moderately small (length < 3mm) and globular (Fig. 36.22) with the anterior clypeal margin unmodified (as in Fig. 36.8c), the posterolateral angles of the pronotum not extending acutely posteriorly (Fig. 36.22), no carinae present on the elytra (Fig. 36.22), and the apex of the prosternal process extending to the metaventrite (as in Fig. 36.1a). Unlike those two genera, the median lobe is deeply and characteristically bifid (Fig. 36.10a).

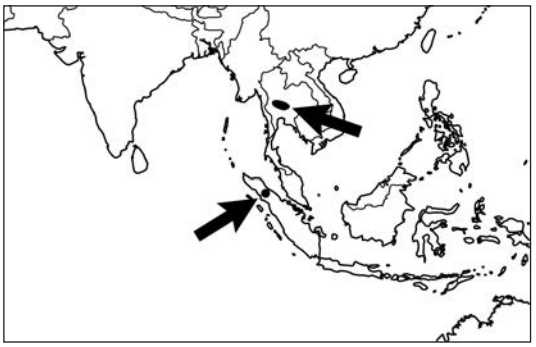
Classification. The group is similar to *Hyphydrus*, and one of the original species, *H. dismorphus* (Biström), described from a female specimen, was first placed in *Hyphydrus*. When males were discovered, the species was found to belong to *Hyphovatus* (Wewalka and Biström, 1994).

Fig. 36.22. *Hyphovatus dismorphus*. Scale = 1.0mm.

Diversity. There are currently three species in this poorly known genus.

Natural History. Species in the group have been collected from slow forest streams.

Distribution. *Hyphovatus* are found in Thailand and Sumatra (Map 36.11). They likely also occur in Malaysia (Balke *et al.*, 2004a).



Map 36.11. Distribution of *Hyphovatus*.

Genus *Hyphydrus* Illiger, 1802

Body Length. 2.5–6.8mm.

Diagnosis. *Hyphydrus* have the following combination within Hyphydrini: (1) the prosternal process is in contact with the anterior margin of the metaventrite (Fig. 36.1a); (2) the posterolateral angles of the pronotum do not acutely project posteriorly (Figs. 36.3b,23); (3) the elytra lack carinae (Fig. 36.23); (4) the metacoxal process lacks a lobe of any kind, the base of the metatrochanter is completely exposed (Fig. 36.1a); and (5) the clypeus has a distinctive anterior marginal bead (Fig. 36.8a, some species have this bead indistinct, and in those taxa the anterior metatibial spur is serrate (Fig. 36.7a)). These are small to medium sized diving beetles that are typically globular and often very attractively maculate or fasciate dorsally (Fig. 36.23).

Classification. *Hyphydrus* is sister group to the five genera in the cape lineage and Madagascan *Hovahydrus* in the analyses by Ribera *et al.* (2008) and Ribera and Balke (2007).

Diversity. This is the largest group in Hyphydrini including 139 species currently. They were revised

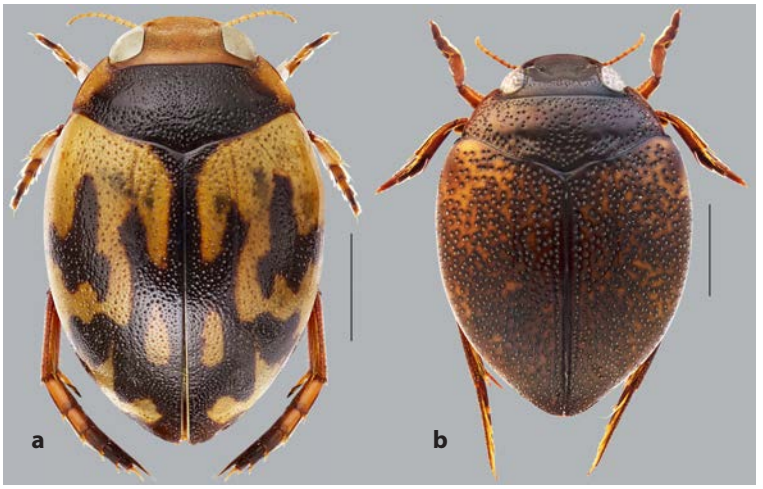


Fig. 36.23. *Hyphydrus* species. **a**, *H. signatus*. **b**, *H. congoanus*. Scales = 1.0mm.

in an exceptional monograph by Biström (1983e), though quite a few additional species have been described since (Biström 1984b–e; 1985c; 1986b; 2000; Biström and Satô, 1988; Wewalka and Biström, 1989; 1993; Biström *et al.,* 1993; 1997b; Stastny, 2000). The Australian fauna was reviewed by Watts and Leys (2006), and the fauna of Myanmar by Shaverdo (2007).

Natural History. *Hyphydrus* occur in many habitats, but mainly ponds and pools with vegetation. They often appear at lights. Larvae were described by Alarie and Watts (2005). Chemical defensive glands and their constituents were described by de Marzo (1977), Baumgarten *et al.* (1997), Nakanishi (2001), and Friis *et al.* (2003). Several additional aspects of their biology and natural history — including dispersal, feeding strategies, and sexual dimorphism — have been investigated by Jackson (1972), Juliano and Lawton (1990a), and Juliano (1992).

Distribution. *Hyphydrus* occur throughout much of the Old World, including all of Africa and Madagascar, much of Europe, across Asia, and south into Australia and New Zealand (Map 36.12). There are species in several archipelagos as well, including the Canaries, Mauritius and Reunion Islands, and many South Pacific islands (Map 36.12).

Map 36.12. Distribution of *Hyphydrus*.

Genus *Microdytes* J. Balfour-Browne, 1946

Body Length. 1.2–2.3mm.

Diagnosis. These beetles have the prosternal process extending to the metaventrite (as in Fig. 36.1a); the pronotum with the posterolateral angles not extended posteriorly (Fig. 36.24); the base of the metatrochanter somewhat obscured by a minute, triangular lobe (Fig. 36.4a); and the prosternal process with a distinct medial prominence (Fig. 36.5a). Members of the group are small to extremely small and globular (Fig. 36.24), though some are somewhat more elongate and dorsoventrally flattened. Some are

Fig. 36.24. *Microdytes sabitae.* Scale = 1.0mm.

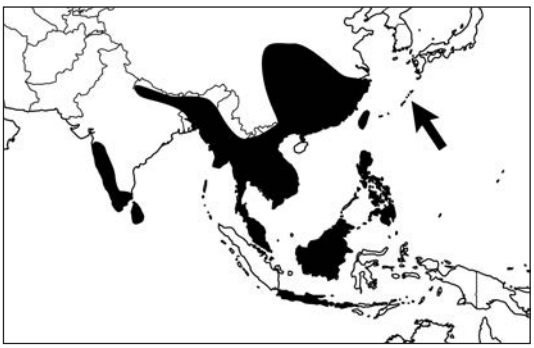
maculate (Fig. 36.24). The subterranean species *M. trontelji* Wewalka *et al.* differs from *Dimitshydrus*, the other subterranean hyphydrine, in being elongate oval and dorsoventrally compressed, rather than short, broadly rounded and globular (Fig. 36.19), and having the eyes reduced and V-shaped instead of absent entirely.

Classification. *Microdytes* are related to *Allopachria* within Hyphydrini (Ribera and Balke, 2007).

Diversity. There are 46 species in the genus. *Microdytes* was revised by Wewalka (1997) with additional new species and records since then (Wewalka, 1998; 2011; Wewalka and Wang, 1998; Miller and Wewalka, 2010).

Natural History. Members of the group are found in small seeps and springs or, occasionally, small streams (Wewalka, 1997). One species is subterranean (Wewalka *et al.,* 2007). Larvae were described by Alarie *et al.* (1997).

Distribution. This is mainly a genus of Southeast Asia with species known from China south into Indonesia and several from India and Sri Lanka (Map 36.13).



Map 36.13. Distribution of *Microdytes*.

Genus *Primospes* Sharp, 1882

Body Length. 4.7–5.0mm.

Diagnosis. *Primospes* have the prosternal process extending to the metaventrite (as in Fig. 36.1a), the clypeus evenly rounded (as in Fig. 36.8c), the metatibial spurs not serrate (as in Fig. 36.7b), the base of the metatrochanter entirely exposed without a concealing lobe (as in Fig. 36.1a), the elytra without carinae (Fig. 36.25), and the pronotum with the posterolateral angles distinctly extended posteriorly (Figs. 36.9a,25). These beetles are moderately large and relatively elongate (Fig. 36.25).

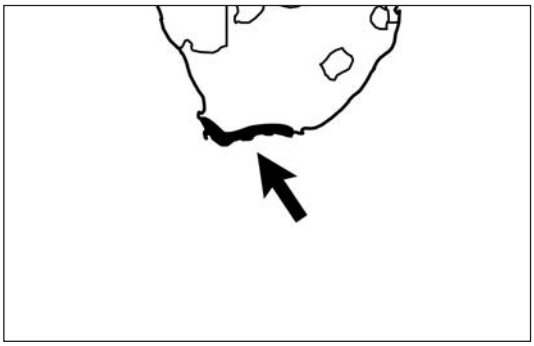
Fig. 36.25. *Primospes suturalis.* Scale = 1.0mm.

Classification. *Primospes* is part of the South African endemic Cape lineage clade of Hyphydrini and sister to *Hydropeplus* + *Andex* (Ribera and Balke, 2007).

Diversity. *Primospes suturalis* Sharp is the only species in the genus.

Natural History. The species has been found in rainwater in a salt marsh (Alarie and Challet, 2006a). Larvae were described (Alarie and Challet, 2006a).

Distribution. *Primospes* are known only from the Cape region of South Africa (Map 36.14).



Map 36.14. Distribution of *Primospes*.

37. Tribe Bidessini

Body Length. 0.9–4.8mm.

Diagnosis. The currently best diagnostic characters for this tribe are features that are not easily accessible without dissection of internal tissues. Two particularly strong synapomorphies defining the tribe are presence of a female spermathecal spine (Fig. 37.1) and presence of five-lobed teeth on the proventriculus (Fig. 37.2). Additional features include the following: (1) most genera have the metacoxae fused to the first visible abdominal sternum; (2) most genera have two- or three-segmented male lateral lobes of the aedeagus (Fig. 37.23); and (3) most genera have the metatibia basally slender and apically gradually expanded (Fig. 37.3). Many members of the group, but not all, have a distinct transverse line across the head posterior to the eyes (Fig. 37.4b), a pair of basal striae (or plicae) on the pronotum (Fig. 37.6b), and/or a corresponding stria (or plica) at the base of each elytron (Fig. 37.6b). This tribe includes many of the smallest of all diving beetles and few are >3mm in length. They are often dorsally maculate or fasciate and range from short and robust to elongate and slender.

Classification. The classification of this large and important group of dytiscids has been addressed by a number of influential authors. The historical definition of this group began with Sharp (1882), who placed a number of taxa, mainly previously placed in *Hydroporus*, in a new tribe based on the fusion of the metacoxae with the first visible abdominal sternum. He believed this to be unique among Dytiscidae, and, with this definition, placed in Bidessini the genera *Pachydrus*, *Heterhydrus,* and *Desmopachria*, which are currently in Hyphydrini and Pachydrini.

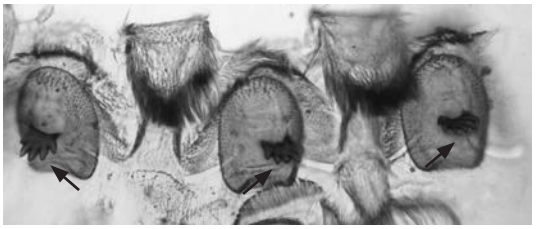


Fig. 37.2. *Peschetius quadricostatus* teeth of proventriculus.

The next main diagnostic effort was by Zimmermann (1919), who defined the group based on the equal-length metatarsal claws and an approximately club-shaped metatiba (e.g., Fig. 37.3), which resulted in removal of *Pachydrus*, *Heterhydrus,* and *Desmopachria* to Hyphydrini. Later influential authors (e.g., Young, 1967a) used a similar character definition for the group. However, in the most comprehensive modern treatment of the group by Biström (1988b), the group was thoroughly reviewed and defined based on the presence of two- (e.g., Fig. 37.17b) or three-segmented (e.g., Fig. 37.17a) male lateral lobes of the aedeagus. This resulted in the exclusion of two genera historically placed in the Bidessini, *Amarodytes* Régimbart and *Hydrodessus* J. Balfour-Browne, which, based on specimens examined by him, lack segmented lateral lobes. He placed these as Hydroporinae *incertae sedis*. During a phylogenetic analysis of the family by Miller (2001c), a new, compelling synapomorphy for the tribe was discovered, a heavily sclerotized spine inside the female spermatheca (Fig. 37.1). Members of *Amarodytes* were found to have such a spine (Miller, 2001c), and the genus was placed by Miller (2001c) back into Bidessini. It was also discovered that at least some

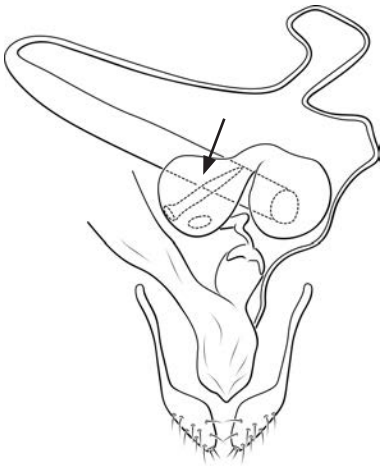


Fig. 37.1. *Peschetius parvus* female reproductive tract, ventral aspect.

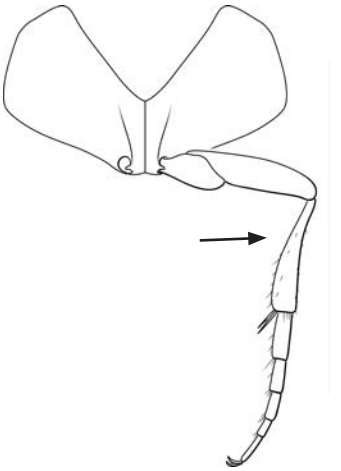


Fig. 37.3. *Uvarus lacustris* metacoxae and left metaleg. Scale = 0.5mm.

species currently attributed to *Amarodytes*, and specifically *A. duponti* (Aubé), have bisegmented lateral lobes (Benetti and Régil Cueto, 2004), though others do not (*Amarodytes* itself may not be monophyletic). Most recently, another synapomorphy was discovered by Miller *et al.* (2006), a five-lobed transverse tooth of the proventriculus (Fig. 37.2). This feature is present in *Amarodytes* and also *Peschetius* Guignot (Miller *et al.,* 2006), a genus previously placed in the Hydroporini. *Peschetius* also has a distinctive spermathecal spine (Fig. 37.1). *Amarodytes* was therefore reconfirmed as a genus of Bidessini, and *Peschetius* was formally moved into Bidessini. Finally, several members of *Hydrodessus* were also found to have a spermathecal spine (though not all do) and the five-lobed, transverse tooth of the proventriculus, and the genus was placed back in Bidessini (Miller and Bergsten, 2014a). It is becoming increasingly evident that Bidessini includes two clades, one united by a single segment in the lateral lobe (including *Peschetius*, *Hydrodessus,* and at least some *Amarodytes*), and the rest of the group in another clade (Miller and Bergsten, 2014a). It should be noted that at least one derived member of Bidessini, the subterranean *Limbodessus insolitus* Watts and Humphreys, has the lateral lobe also with a single segment (Watts and Humphreys, 2009). The knowledge on the phylogeny of genera in the group is otherwise fragmentary, and monophyly of some of the genera is questionable. A major problem with the group is that genera diagnoses rely on relatively few characters that come in many different combinations. At the same time it is becoming clear that several of the most important characters used in the generic classification are highly homoplasious.

Diversity. There are 47 bidessine genera with new ones described regularly. Significant generic revision is expected in the near future, and this number will likely change. This is the largest group in Dytiscidae with about 16% of currently recognized species (see Fig. 2.3, Nilsson, 2001; 2003c; 2004; Nilsson and Fery, 2006), and probably many more unknown species.

Natural History. Bidessini occur in a great many habitats though most are lentic, particularly in shallow margins, which may have huge numbers of specimens and numerous species. Some species are lotic, particularly in sandy streams, and others are in hygropetric habitats, phytotelmata, subterranean aquifers, and terrestrial leaf-litter habitats. There are many specialists. Large numbers of specimens, and a diversity of species, come to lights.

Distribution. Bidessines occur throughout the world, though they are considerably less diverse at high latitudes or high elevations. They are most abundant and speciose in tropical lowlands.

Key to the Epigean Genera of Bidessini

Sinodytes, Comaldessus, *Trogloguignotus*, many *Limbodessus* species, some *Neobidessodes,* and one species of *Uvarus* are subterranean. These have features common to other subterranean diving beetles (see Fig. 3.51, flightless, eyeless, depigmented) and are keyed separately (page 45). *Geodessus* may be at least partly terrestrial, but specimens are more typical of Bidessini and are keyed below.

1 Occipital line absent (Fig. 37.4a) 2
1' Occipital line present (Fig. 37.4b). 24

2(1) Transverse epipleural carina present at humeral angle (Fig. 37.5a);. Australia, Southeast Asia (Map 37.26). . . . . *Limbodessus* (in part), 244
2' Epipleural carina absent (Fig. 37.5b) 3

3(2) Elytral striae absent (Fig. 37.6a,c). 4
3' Elytral striae present (Fig. 37.6b) 14

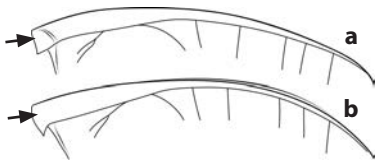


Fig. 37.5. Bidessini left elytral epipleuron. **a**, *Limbodessus compactus*. **b**, *Peschetius parvus*.

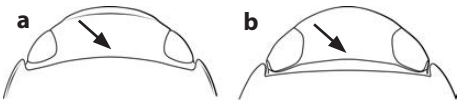


Fig. 37.4. Bidessini heads. **a**, *Petrodessus conatus*. **b**, *Liodessus affinis*.

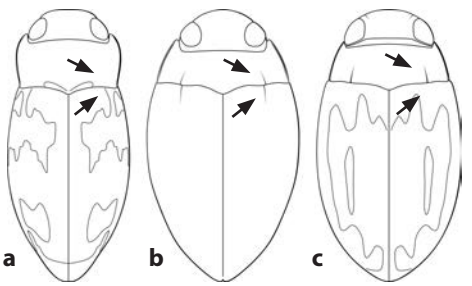


Fig. 37.6. Bidessini habitus. **a**, *Hydrodessus surinamensis*. **b**, *Uvarus granarius*. **c**, *Incomptodessus camachoi.*

4(3) Pronotal striae absent (Fig. 37.6a). 5
4' Pronotal striae present (Fig. 37.6b,c) 8

5(4) With prominent longitudinal, sublateral carinae on elytron (Fig. 37.7a); abdomen distinctly medially tectiform (Fig. 37.7b); with large punctures on the dorsal and ventral surfaces (Fig. 37.7b); Africa, India (Map 37.34) . . . . . *Peschetius*, 250
5' No longitudinal, medial carinae on elytron; abdomen not tectiform; body surfaces often punctate, but punctures not unusually large 6

6(5) With longitudinal lateral carina extending from humeral angle along lateral surface of elytron (Fig. 37.8a) or with longitudinal carinae on lateral surfaces of metaventrite (Fig. 37.8b) or with both; Neotropical (Map 37.20) . . . . . *Hydrodessus*, 240
6' Without carina at humeral angle on elytron or on metaventrite 7

7(6) Elytra maculate (Fig. 37.66); posterior margin of abdominal sternite VI without continuous bead (Fig. 37.9a); Neotropical (Map 37.22) . . . . . *Hypodessus*, 241
7' Elytra black, immaculate (Fig. 37.85); posterior margin of abdominal sternite strongly and continuously beaded (Fig. 37.9b); Venezuela (Map 37.41). . . . . *Tepuidessus*, 254

8(4) Natatory setae absent on legs (Fig. 37.10a) . 9
8' Natatory setae present on legs, at least on metatiba (Fig. 37.10b). 10

9(8) Body shape elongate oval (Fig. 37.11a); lateral pronotal bead narrow (Fig. 37.11a); Nepal, India (Map 37.15). . . . . *Geodessus*, 237
9' Body shape robust (Fig. 37.11b); lateral pronotal bead broad (Fig. 37.11b); northern South America (Map 37.40) . . *Spanglerodessus*, 253

10(8) Pronotal striae short and distinctly curved (Fig. 37.12a); dorsal coloration fasciate or maculate (Fig. 37.47); Neotropical (Map 37.3) . . . . . *Amarodytes*, 229
10' Pronotal striae straight or sinuate (Fig. 37.12b); dorsal coloration various 11

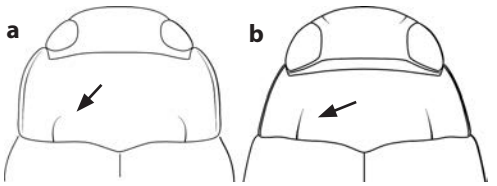


Fig. 37.12. Bidessini heads and pronota. **a**, *Amarodytes* sp. **b**, *Liodessus affinis*.

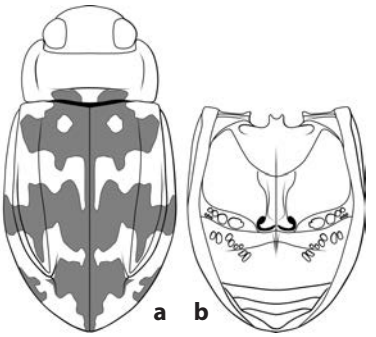


Fig. 37.7. *Peschetius parvus.* **a**, dorsal; **b**, ventral.

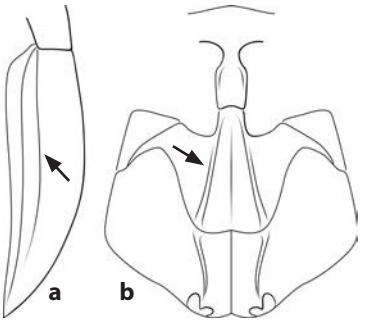


Fig. 37.8. *Hydrodessus angularis*. **a**, Elytron, lateral aspect. **b**, Ventral thoracic surfaces.

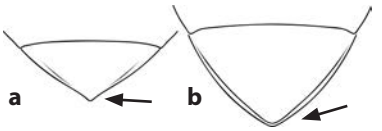


Fig. 37.9. Bidessini last abdominal sternites. **a**, *Hypodessus frustrator*. **b**, *Tepuidessus breweri*.

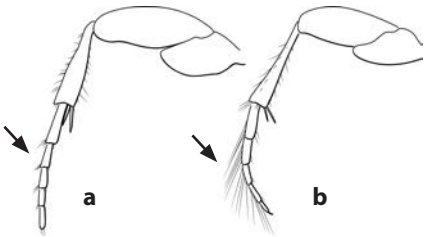


Fig. 37.10. Bidessini right metaleg. **a**, *Spanglerodessus shorti.* **b**, *Fontidessus toboganensis*.

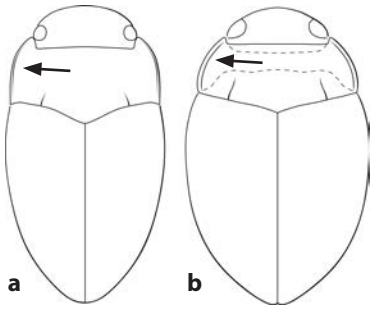


Fig. 37.11. Bidessini habitus, **a**, *Geodessus kejvali*. **b**, *Spanglerodessus shorti*.

11(10) Anterior clypeal margin modified, angulate, and margined in male (Fig. 37.13a); body shape globular and posteriorly attenuate (Fig. 37.13a); Borneo (Map 37.9) . . . . . *Borneodessus*, 233

11' Anterior clypeal margin unmodified in both sexes (Fig. 37.13b); body shape variable, but if attenuate posteriorly, then elongate oval (Fig. 37.13b,c) 12

12(11) With series of minute denticles along posterior margins of abdominal ventrites III–V (Fig. 37.14); Neotropical (Map 37.6) . . . . . *Bidessodes*, 231

12' Without denticles along posterior margin of abdominal ventrites 13

13(12) Body robust, broadly oval, posteriorly rounded (Fig. 37.13b); male median lobe with distinctive, separate ventral sclerite (Fig. 37.15); Neotropical (Map 37.14) . . . . . *Fontidessus*, 236

13' Body elongate oval, posteriorly attenuate (Fig. 37.13c); male median lobe without ventral sclerite; Australian (Map 37.29) . . . . . *Neobidessodes*, 246

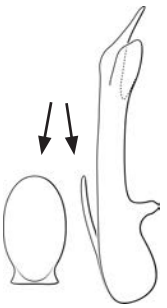


Fig. 37.15. *Fontidessus ornatus* male median lobe.

14(3) Sutural lines present on elytron (Fig. 37.16a) 15

14' Sutural lines absent on elytron (Fig. 37.16b) 17

15(14) Body shape elongate, flattened, pronotum widest anterior of middle (Fig. 37.16c); Middle East (Map 37.17) . . . . . *Glareadessus*, 238

15' Body shape elongate oval, pronotum widest at or near posterior margin (Fig. 37.16a). 16

16(15) Lateral lobes with three segments (Fig. 37.17a); Europe, Africa, Asia to Australia (Map 37.21). . . . . *Hydroglyphus*, 240

16' Lateral lobes with two segments (as in Fig. 37.17b); Central and South America . . . . . *Uvarus* (in part) *spretus*, 256

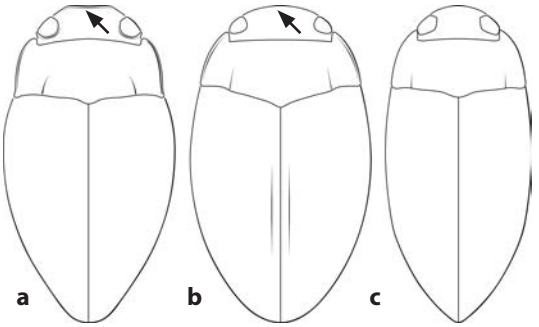


Fig. 37.13. Bidessini habitus, **a**, *Borneodess zetteli*. **b**, *Fontidessus toboganensis*. **c**, *Neobidessodes thoracicus*.

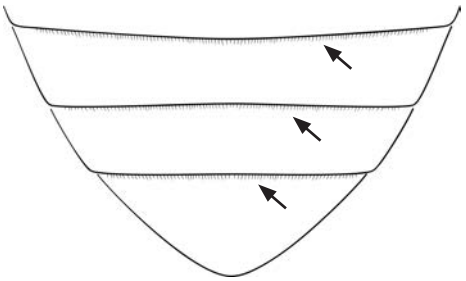


Fig. 37.14. *Bidessodes knischi* abdominal ventrites.

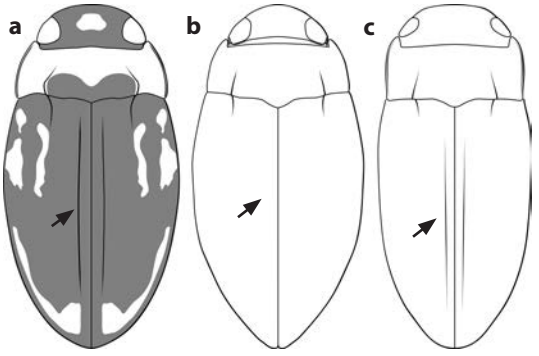


Fig. 37.16. Bidessini habitus, **a**, *Hydroglyphus japonicus*. **b**, *Liodessus affinis*. **c**, *Glareadessus stocki*.

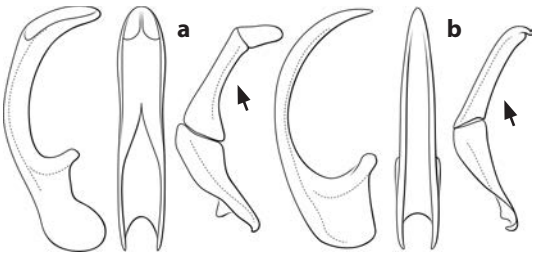


Fig. 37.17. Bidessini male genitalia, median lobe right lateral aspect, median lobe ventral aspect, right lateral lobe, lateral aspect. **a**, *Hydroglyphus lineolatus*. **b**, *Liodessus affinis*.

17(14) Elytron with two moderately distinct longitudinal discal impressed lines of punctures in addition to other punctures on elytron (Fig. 37.18); New Zealand (Map 37.19) . . . . . *Huxelhydrus*, 239

17' Elytron without longitudinal rows of punctures 18

18(17) Anterior clypeal margin flattened, produced or beaded (Fig. 37.19a) 19

18' Anterior clypeal margin rounded, not modified (Fig. 37.19b) 20

19(18) Elytra maculate (Fig. 37.49); northern South America (Map 37.5) . . . . . *Belladessus*, 230

19' Elytra evenly colored (Fig. 37.79); Australia (Map 37.35) . . . . . *Petrodessus*, 250

20(18) Metatrochanter short, apically strongly rounded, and offset (Fig. 37.20a); male median lobe complicated, with multiple apical branches, lateral lobe apically broad and broadly rounded (Fig. 37.21); northern Neotropical (Map 37.47) . . . . . *Zimpherus*, 258

20' Metatrochanter variable, not apically strongly rounded and offset (Fig. 37.20b); male median lobe various 21

21(20) Body length minute (~1.5mm); median lobe terminating in four processes (Fig. 37.22); Neotropical (Map 37.28) . . . *Microdessus*, 246

21' Body length larger (>1.5mm); median lobe not terminating in four processes 22

22(21) Lateral lobes with three segments (Fig. 37.23a); Africa (Map 37.37) *Pseuduvarus*, 251

22' Lateral lobes with two segments (Fig. 37.23b,c) 23

23(22) Lateral lobe apically with tooth-shaped lobe (Fig. 37.23b); Nearctic, Neotropical, Afrotropical, Oriental (Map 37.44) . . . . . *Uvarus* (in part), 256

23' Lateral lobe apically simply rounded (Fig. 37.23c); New Guinea (Map 37.33) . . . . . *Papuadessus*, 249

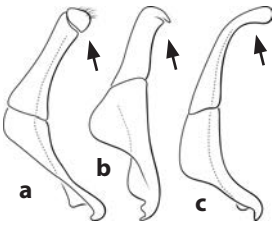


Fig. 37.23. Bidessini male lateral lobe, lateral aspect. **a**, *Pseuduvarus vitticollis*. **b**, *Uvarus lacustris*. **c**, *Papuadessus baueri.*

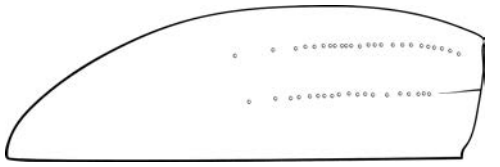


Fig. 37.18. *Huxelhydrus syntheticus* left elytron.

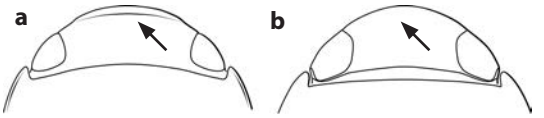


Fig. 37.19. Bidessini heads. **a**, *Petrodessus conatus*. **b**, *Uvarus granarius*.

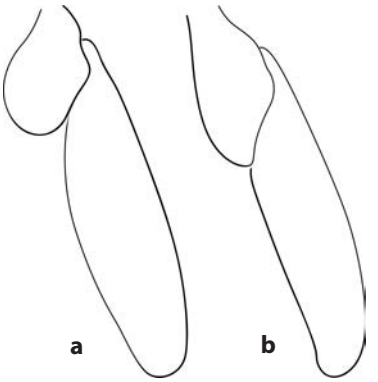


Fig. 37.20. Bidessini right metatrochanter and metafemur. **a**, *Zimpherus nancae*. **b**, *Uvarus lacustris*.

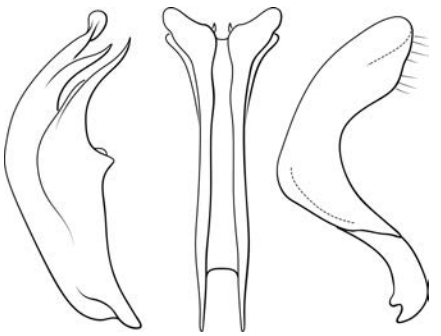


Fig. 37.21. *Zimpherus nancae* male genitalia, median lobe right lateral aspect, median lobe ventral aspect, right lateral lobe lateral aspect.

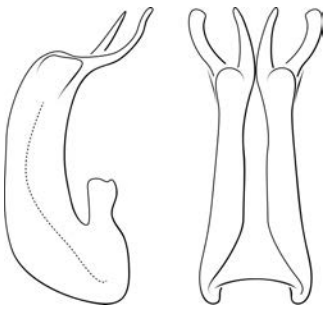


Fig. 37.22. *Microdessus atomarius* male median lobe right lateral and ventral aspects.

24(1) With longitudinal carinae present on disc of elytron (Fig. 37.24a,b,d,e) 25
24' Without longitudinal carinae on elytron . . . 30

25(24) With incomplete transverse carina across epipleuron at humeral angle (Fig. 37.28d); Madagascar (Map 37.32) . . . . . *Pachynectes* (in part) (*Yoloides*), 248
25' Without transverse carina across eipleuron at humeral angle (as in Fig. 37.28b), or not Madagascar 26

26(25) Elytron with only a lateral carina (Fig. 37.24a); Afrotropical (Map 37.1) . . . . . *Africodytes,* 228
26' Elytron with a discal keel (Fig. 37.24b,d,e) 27

27(26) Elytra without longitudinal series of punctures (Fig. 37.24d) 28
27' Elytra with longitudinal series of punctures (Fig. 37.24e) 29

28(27) Only discal carina present on elytron (Fig. 37.24b); apex of male median lobe trifid (Fig. 37.25a); South Africa (Map 37.38) . . . . . *Sharphydrus* (in part), 252
28' Discal and lateral carinae present on elytron (Fig. 37.24d); apex of male median lobe variable, but not trifid; southern Europe, Afrotropical to India (Map 37.45) . . . . . *Yola*, 257

29(27) Pronotal striae connected by an impunctate furrow (Fig. 37.24e); Nearctic and Neotropical (Map 37.4) . . . . . *Anodocheilus*, 229
29' Pronotal striae not connected by impunctate furrow (Fig. 37.24c); Afrotropical (Map 37.46) . . . . . *Yolina*, 257

30(24) Basal eytral striae present (Fig. 37.26a) . 31
30' Basal elytral striae absent (Fig. 37.26b) . . . 43

31(30) Anterior clypeal margin modified, flattened, beaded, and/or protruding (Fig. 37.27a) . . . 32
31' Clypeal margin unmodified (Fig. 37.27b) . . 35

32(31) Elytral epipleuron with transverse carina at humeral angle (Fig. 37.28a); Africa, southern and southeastern Asia, Australia (Map 37.11) . . . . . *Clypeodytes* (in part), 234
32' Elytral epipleuron without transverse carina at humeral angle, or only weak (Fig. 37.28b,d) 33

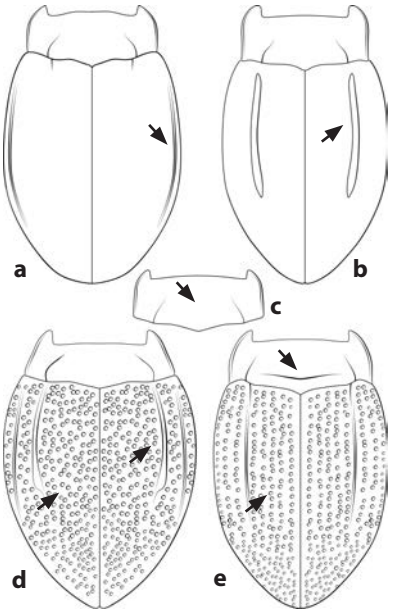


Fig. 37.24. Bidessini dorsal surfaces. **a**, *Africodytes rubromaculatus*. **b**, *Sharphydrus capensis*. **c**, *Yolina wewalkai*. **d**, *Yola tuberculata*. **e**, *Anodocheilus maculatus.*

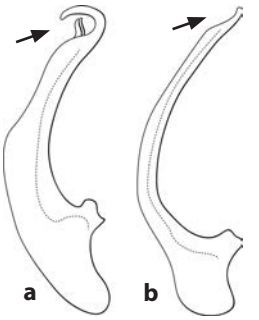


Fig. 37.25. Bidessini male median lobe, lateral aspect. **a**, *Sharphydrus coriaceus*. **b**, *Yola tuberculata.*

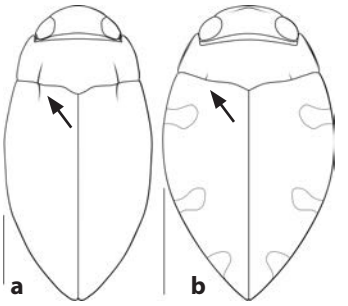


Fig. 37.26. Bidessini habitus, **a**, *Liodessus affinis*. **b**, *Hemibidessus conicus*. Scales = 1.0mm.

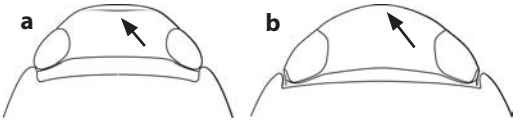


Fig. 37.27. Bidessini heads, **a**, *Neoclypeodytes ornatellus*. **b**, *Liodessus affinis*.

33(32) Metaventrite without series of punctures (Fig. 37.28b); North and Central America (Map. 37.31) . . . . . *Neoclypeodytes*, 247
33' Metaventrite with longitudinal series of punctures at midline (Fig. 37.28c) 34

34(33) Body shape globular, robust (Fig. 37.29a); Africa, southern and southeastern Asia, Australia (Map 37.25) . . . . . *Leiodytes* (in part), 243
34' Body shape elongate, flattened (Fig. 37.29b); Australia (Map 37.24) . . . . *Kakadudessus*, 242

35(31) Elytron with accessory stria between suture and elytral stria (Fig. 37.30a, sometimes difficult to discern); Nearctic and Neotropical (Map 37.30). . . . . *Neobidessus*, 247
35' Elytron without accessory stria between suture and elytral stria (Fig. 37.30b) 36

36(35) Tarsi distinctly pentamerous, tarsomere IV elongate and prominent (Fig. 37.31a); male with ventral surface concave medially (Fig. 37.32a); male mesotibia curved (Fig. 37.33a); Nearctic and Neotropical (Map 37.7) . . . . . *Bidessonotus*, 231
36' Tarsi distinctly pseudotetramerous, tarsomere IV located within lobes of III (Fig. 37.31b); male with ventral surface convex (Fig. 37.32b); male mesotibia relatively straight (Fig. 37.33b). 37

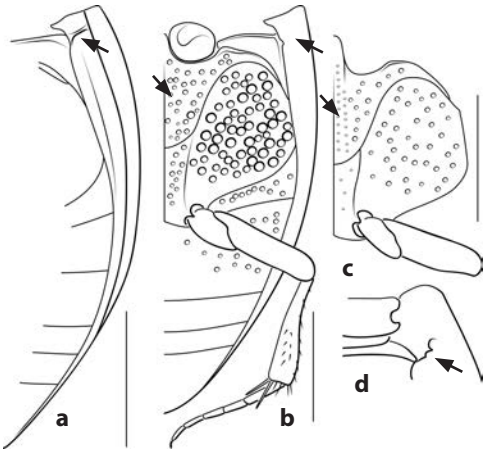


Fig. 37.28. Bidessini ventral surfaces. **a**, *Clypeodytes bedeli*. **b**, *Neoclypeodytes cinctellus*. **c**, *Leiodytes hieroglyphicus*. **d**, *Pachynectes hygrotoides*. Scales = 0.5mm.

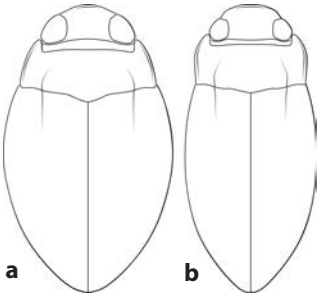


Fig. 37.29. Bidessini habitus. **a**, *Leiodytes evanescens*. **b**, *Kakadudessus tomweiri*.

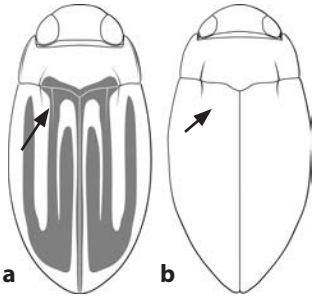


Fig. 37.30. Bidessini habitus. **a**, *Neobidessus pullus*. **b**, *Liodessus affinis*.

Fig. 37.32. Bidessini lateral habitus. **a**, *Bidessonotus tibialis*. **b**, *Allodessus bistrigatus*.

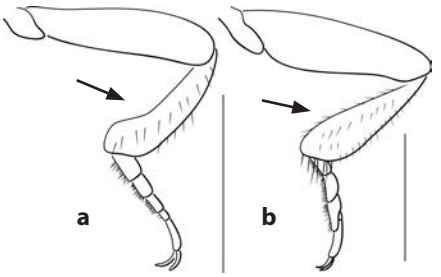


Fig. 37.33. Bidessini mesolegs. **a**, *Bidessonotus obtusatus*. **b**, *Allodessus bistrigatus*. Scales = 0.5mm.

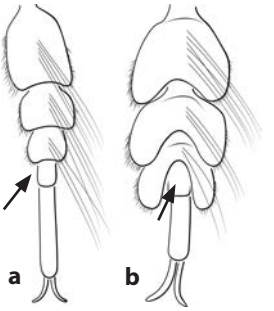


Fig. 37.31. Bidessini male protarsi. **a**, *Bidessonotus obtusatus*. **b**, *Allodessus bistrigatus*.

37(36) Metacoxal lines short, width of combined medial portions of metacoxa = length (Fig. 37.34a); Australia (Map 37.16) . . . . . .*Gibbidessus,* 237

37' Metacoxal lines long, combined width of medial portions of metacoxa < length (Fig. 37.34b) 38

38(37) Apex of lateral lobe slender, hooked (Fig. 37.35a); Australia and southeast Asia (Map 37.2). . . . . .*Allodessus*, 228

38' Apex of lateral lobe various (e.g., Fig. 37.35b), but not slender and hooked as in Fig. 37.35a 39

39(38) Elytral sutural line well developed (Fig. 37.36a); Europe, Africa, southern and southeastern Asia, Australia (Map 37.8) . . . . . *Bidessus*, 232

39' Elytral sutural line absent or with only a linear series of punctures (Fig. 37.36b). 40

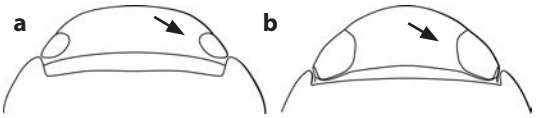


Fig. 37.37. Bidessini heads. **a**, *Crinodessus amyae.* **b**, *Liodessus affinis.*

40(39) Eyes small (head width/distance between eyes = 1.3, Fig. 37.37a); Nearctic (Map 37.13) . . . . . *Crinodessus*, 235

40' Eyes large (head width/distance between eyes = 1.8, Fig. 37.37b). 41

41(40) Male lateral lobe robust, apical segment broad, with elongate hook-shaped lobe (Fig. 37.38). . . . . *Limbodessus* (in part), 244

41' Male lateral lobe variable but not broad, without apical elongate hook-shaped lobe 42

42(41) Body shape elongate oval (Fig. 37.39a); Nearctic, Neotropical, Afrotropical (Map 37.27) . . . . . *Liodessus*, 245

42' Body shape golobular (Fig. 37.39b); Africa, southern and southeastern Asia, Australia (Map 37.25). . . . . .*Leiodytes* (in part), 243

Fig. 37.38. *Limbodessus compactus*, male lateral lobe.

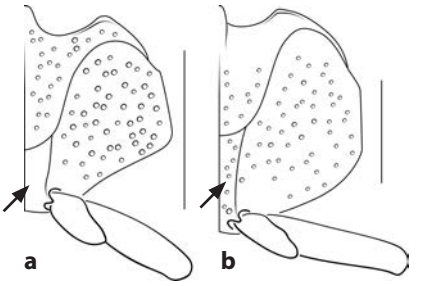


Fig. 37.34. Bidessini left metacoxa. **a**, *Gibbidessus chipi*. **b**, *Allodessus bistrigatus*. Scales = 0.5mm.

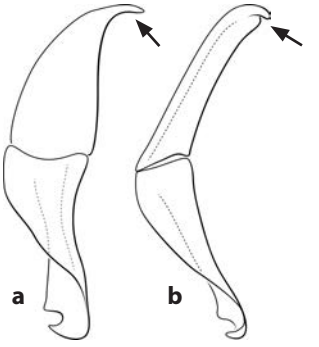


Fig. 37.35. Bidessini male genitalia, male lateral lobe right lateral aspect. **a**, *Allodessus bistrigatus.* **b**, *Liodessus affinis*.

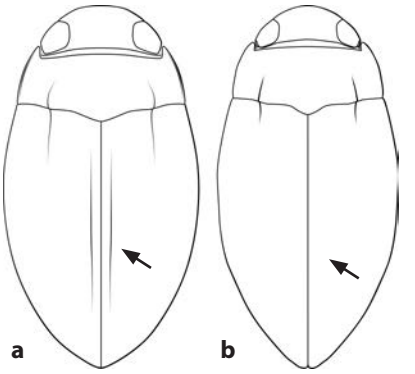


Fig. 37.36. Bidessini habitus. **a**, *Bidessus toumodiensis*. **b**, *Liodessus affinis.*

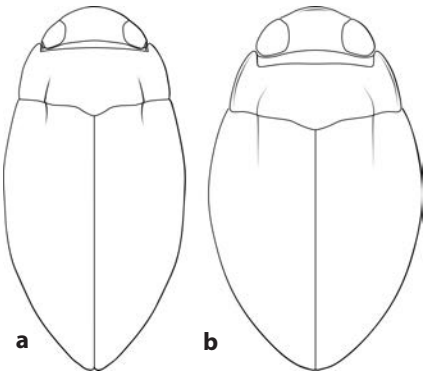


Fig. 37.39. Bidessini habitus. **a**, *Liodessus affinis*. **b**, *Leiodytes evanescens*.

43(30) Prosternal process not extending between mesocoxa to metaventrite (Fig. 37.40a); southern Africa (Map 37.43) . . . *Tyndallhydrus*, 255
43' Prosternal process extending between mesocoxa to metaventrite (Fig. 37.40b) 44

44(43) Anterior clypeal margin modified, flattened, protruding, or beaded (Fig. 37.41a,b) 45
44' Anterior clypeal margin not modified (Fig. 37.41c). 48

45(44) Epipleuron without transverse carina at humeral angle (Fig. 37.42a); Africa (Map 37.36) . . . . . *Platydytes*, 251
45' Epipleuron with transverse carina at humeral angle (Fig. 37.42b) 46

46(45) Anterior clypeal margin with two prominences, one on each side (Fig. 37.41a); Nearctic and Neotropical (Map 37.10) . . . . . *Brachyvatus*, 233
46' Anterior clypeal margin without prominences (Fig. 37.41b) 47

47(46) Pronotal striae very short or nearly absent (Fig. 37.43a); Neotropical (Map 37.18) . . . . . *Hemibidessus*, 238
47' Pronotal striae long and distinct (Fig. 37.43b) . . .*Clypeodytes* (in part) (*Hypoclypeus*) and *C.* (*Paraclypeus*)

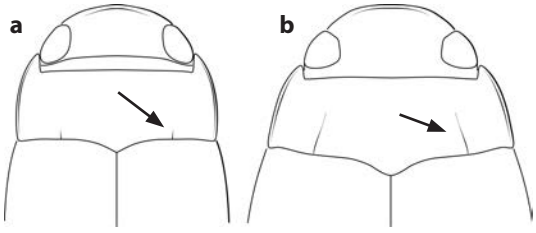


Fig. 37.43. Bidessini heads and pronota. **a**, *Hemibidessus celinoides*. **b**, *Clypeodytes hemani*.

48(44) Metaventrite with lateral keels (Fig. 37.44a); Madagascar (Map 37.32) . . . . . .*Pachynectes* (in part) *s. str.*, 248
48' Metaventrite without lateral keels (Fig. 37.44b,c) 49

49(48) Metacoxae and metaventrite nearly impunctate (Fig. 37.44b); Neotropical (Map 37.23) . . . . . .*Incomptodessus*, 242
49' Metacoxae and metaventrite puncate (Fig. 37.44c); South Africa (Map 37.38) . . . . . *Sharphydrus* (in part), 252

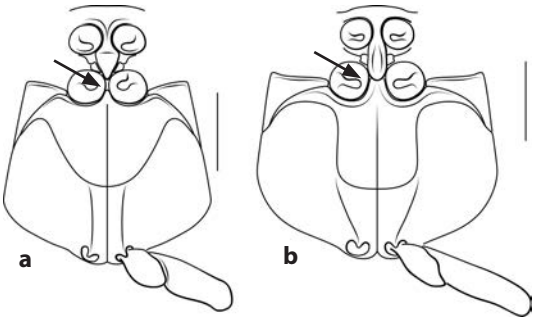


Fig. 37.40. Bidessini ventral surfaces. **a**, *Tyndallhydrus caraboides*. **b**, *Hemibidessus bifasciatus*. Scales = 1.0mm.

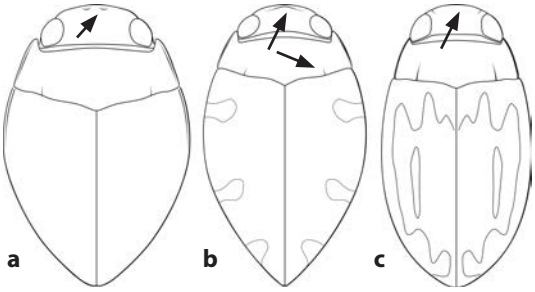


Fig. 37.41. Bidessini habitus. **a**, *Brachyvatus acuminatus*. **b**, *Hemibidessus conicus*. **c**, *Incomptodessus camachoi*.

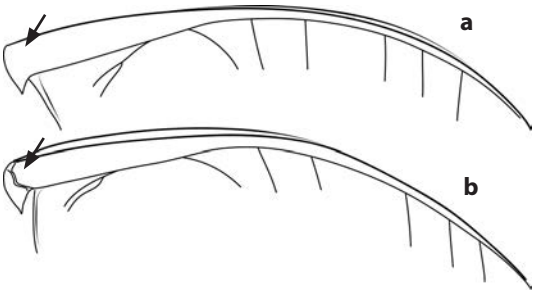


Fig. 37.42. Bidessini left elytral epipleuron. **a**, *Platydytes coarctaticollis*. **b**, *Hemibidessus conicus*.

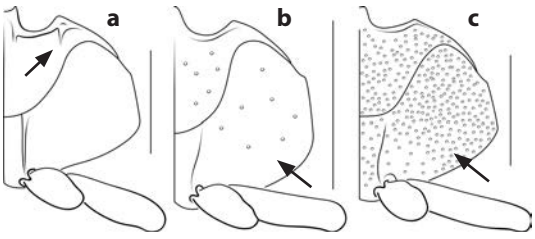


Fig. 37.44. Bidessini ventral surfaces. **a**, *Pachynectes* sp. **b**, *Incomptodessus camachoi*. **c**, *Sharphydrus kamiesbergensis*. Scales = 0.5mm.

Fig. 37.45. *Africodytes rubromaculatus*. Scale = 1.0mm.

Genus *Africodytes* Biström, 1988

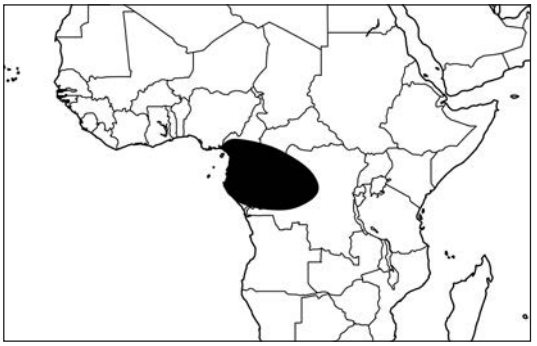
Body Length. 2.0–2.7mm.

Diagnosis. *Africodytes* is characterized by the following character combination (Fig. 37.45): (1) the head with a transverse occipital line; (2) the anterior clypeal margin unmodified; (3) the pronotum with a pair of basal striae; (4) each elytron with a basal stria; (5) the elytron without a sutural stria; (6) the epipleuron without a transverse carina at the humeral angle; and (7) the elytron with a distinct lateral carina extending posteriorly about half the length of the elytron. Specimens are robust and often attractively marked (Fig. 37.45).

Classification. Biström (1988b) placed the genus near *Yola*, *Yolina,* and *Anodocheilus* based on the presence of elytra carinae.

Diversity. There are five species currently assigned to *Africodytes*. The genus has not been comprehensively revised.

Natural History. Specimens have been collected in small forest pools (Bilardo and Rocchi, 1999). They are relatively rare in collections.



Map 37.1. Distribution of *Africodytes*.

Distribution. The species in *Africodytes* are found in central Africa (Map 37.1).

Genus *Allodessus* Guignot, 1953

Body Length. 2.1–3.5mm.

Diagnosis. This genus is characterized among Bidessini by the following (Fig. 37.46): (1) a transverse occipital line present across the head; (2) the anterior clypeal margin unmodified; (3) a basal stria present on each elytron; (4) a pair of basal pronotal striae present; (5) a sutural stria absent on the elytron; (6) without a transverse carina across the epipleuron at the humeral angle; (7) two-segmented male lateral lobes with the apex slender and somewhat hooked; and (8) the male median lobe elongate, slender, and shallowly curved. Specimens are moderately large and elongate oval (Fig. 37.46).

Classification. Historically there was a single species in the genus, *A. bistrigatus* (Clark), which was originally described in *Hydroporus* and then placed in *Bidessus* (Sharp, 1882) until Guignot (1953) placed it in a new genus. However, several additional species previously placed in *Liodessus* were transferred into *Allodessus* by Balke and Ribera (2004).

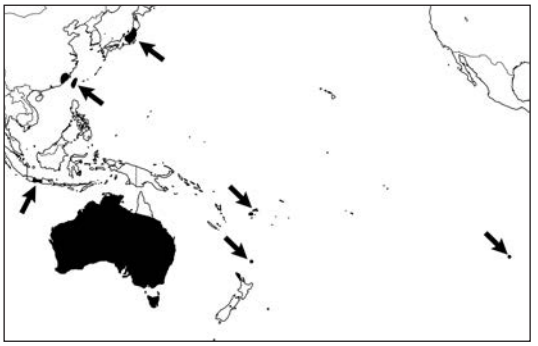
Diversity. Currently five species are classified in *Allodessus*.

Natural History. *Allodessus* are found in a variety of habitats, but especially temporary or semipermanent, muddy-bottomed lentic pools and ponds. They can be extremely abundant and often come to lights in large numbers. Some species are known from brackish, estuarine habitats (Satô, 1964). Larvae

Fig. 37.46. *Allodessus bistrigatus*. Scale = 1.0mm.

have been described by Michat *et al.* (2011).

Distribution. *Allodessus* are found throughout much of Australia and sporadically in other areas of Southeast Asia from Japan south to Indonesia and on certain remote oceanic islands (Map 37.2).



Map 37.2. Distribution of *Allodessus*.

Genus *Amarodytes* Régimbart, 1900

Body Length. 2.0–3.0mm.

Diagnosis. This genus is characterized among Bidessini by the following (Figs. 37.12a,47): (1) the transverse occipital line is absent; (2) the anterior clypeal margin unmodified; (3) the basal pronotal striae is present, often well-incised and abruptly curved, and located more laterad than in other bidessine genera; (4) the basal elytral striae absent; (5) the elytral sutural stria absent; (6) the male lateral lobe one- or two-segmented; and (7) no transverse carina across the epipleuron at the humeral angle. Members of the group are elongate and typically attractively patterned, fasciate or maculate (Fig. 37.47).

Fig. 37.47. *Amarodytes* sp. Scale = 1.0mm.

Classification. Historically placed in the Bidessini (Young, 1967a; 1969), the genus was excluded from the tribe by Biström (1988b) based on presence of a one-segmented male lateral lobe. At least some species, however, appear to have a two-segmented lateral lobe (Benetti and Régil Cueto, 2004). Additionally, specimens have a distinctive spermathecal spine (as in Fig. 37.1) and five-lobed teeth on the proventriculus (Fig. 37.2). Based on this evidence, the genus was placed back in Bidessini (Miller, 2001c; Benetti and Régil Cueto, 2004; Miller *et al.*, 2006), though monophyly of the genus has not been tested. Members of the group are related to the Neotropical genus *Hydrodessus* and the Afrotropical and Oriental genus *Peschetius* (Miller and Bergsten, 2014a).

Diversity. There are currently 10 species recognized in *Amarodytes*. They have never been revised.

Natural History. Species in this group are characteristic of tropical streams with detritus as well as open rocky or sandy streams. They often come to lights. Larvae have been described by Michat and Alarie (2006).

Distribution. These species are known from lowland South America (Map 37.3) with most of the diversity in the northern part of the continent.

Map 37.3. Distribution of *Amarodytes*.

Genus *Anodocheilus* Babington, 1841

Body Length. 1.3–2.1mm.

Diagnosis. This genus is characterized among Bidessini by the following (Figs. 37.24e,48): (1) a transverse occipital line present; (2) a basal elytral stria present on each elytron; (3) a pair of basal pronotal striae present; (4) the basal pronotal striae connected by a transverse furrow that is impunctate;

Fig. 37.48. *Anodocheilus maculatus.* Scale = 1.0mm.

(5) an elytral sutural stria absent; (6) the male lateral lobes two-segmented; (7) without a transverse carina across the epipleuron at the humeral angle; (8) the elytra with prominent longitudinal carinae on the disc; and (9) with a linear series of punctures on the elytron. These beetles are often robust and irregularly maculate or fasciate, though some are concolorous gray, brown, or black (Fig. 37.48). This genus is very similar to *Yola* and *Yolina* but differs from them in having the basal pronotal striae connected by a transverse furrow (Fig. 37.24e) and (from *Yola*) in having a linear series of punctures on the elytron (Fig. 37.24e).

Classification. Based on the presence of elytral carinae, Biström (1988b) associated this genus with *Yola*, *Yolina,* and *Africodytes*.

Diversity. There are currently 22 species in this group. The genus was revised, with the addition of numerous new species, by Young (1974). Recently, García (2009) described four additional new species.

Natural History. Members of this group are found in a variety of primarily lentic habitats from marshes with emergent vegetation to open, sunny pools with mineral substrates. They occasionally come to lights, and sometimes in exceptional numbers (Young, 1974).

Distribution. *Anodocheilus* is found in eastern North America through parts of Mexico, Central America, the Caribbean, and throughout lowland South America (Map 37.4).

Map 37.4. Distribution of *Anodocheilus*.

Genus *Belladessus* Miller and Short, 2015

Body Length. 2.0–2.1mm.

Diagnosis. This genus is characterized among Bidessini by the following (Fig. 37.49): (1) the transverse occipital line is absent; (2) the anterior clypeal margin is beaded; (3) the basal pronotal striae is present; (4) the basal elytral stria is present; (5) the elytral sutural stria is absent; and (6) there is no transverse carina across the epipleuron at the humeral elytral angle. Known members of the genus are robust and dorsally maculate (Fig. 37.49). Only series of females are known, and the species may be parthenogenetic.

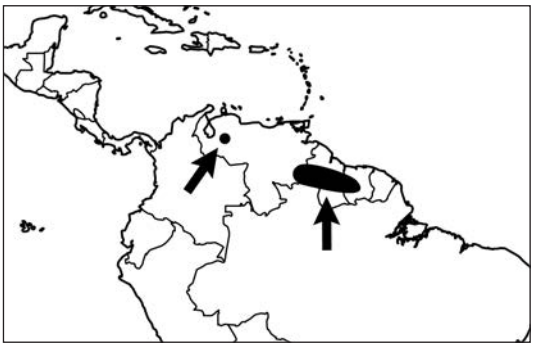
Classification. Relationships with other genera of the tribe are unknown.

Diversity. There are two closely related species in the genus, *B. femineus* Miller and Short and *B. puella* Miller and Short.

Natural History. Only a few specimens of *B. puella* are known, but all are female. Large series of *B. femineus* are known, and all of these are female as well. Miller and Short (2015) suggested that the species may be parthenogenetic. Specimens were collected from forest pools (Miller and Short, 2015).

Fig. 37.49. *Belladessus femineus.* Scale = 1.0mm.

Distribution. This genus is found in northern South America (Map 37.5).



Map 37.5. Distribution of *Belladessus*.

Genus *Bidessodes* Régimbart, 1895

Body Length. 2.0–3.2mm.

Diagnosis. This genus is characterized among Bidessini by the following (Fig. 37.50): (1) the transverse occipital line is absent; (2) the anterior clypeal margin is unmodified; (3) the basal pronotal striae is present; (4) the basal elytral stria is absent; (5) the elytral sutural stria is absent; and (6) there is no transverse carina across the epipleuron at the humeral elytral angle. The genus is very similar to *Neobidessodes*, but *Bidessodes* has a series of fine denticles along the posterior margins of abdominal ventrites III–V (Fig. 37.14). Specimens are elongate oval and often dorsally longitudinally fasciate (Fig. 37.50). Many have dramatically modified male genitalia.

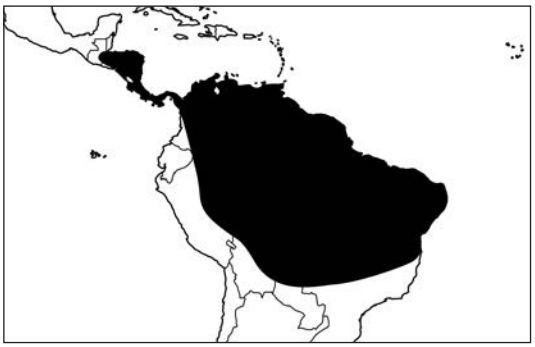
Fig. 37.50. *Bidessodes knishii*. Scale = 1.0mm.

Classification. This group has undergone several changes in classification. It was originally described as a genus (Régimbart, 1900), then placed as a subgenus of *Bidessus* (Zimmermann, 1919; 1920), and then recognized as a genus again (Guignot, 1958). Spangler (1981b) erected two new genera, *Hughbosdinius* Spangler (with one species, *H. leechi* (Spangler) = *B.* (*H.) knischi* Zimmermann) and *Youngulus* Spangler (also with one species, *H.* (*Y.) franki* Spangler), that Young (1986b) later placed as subgenera of *Bidessodes*. Young (1986b) also placed an additional species in *B.* (*Hughbosdinius*) (*B.* (*H.*) *obscuripennis* Zimmermann)). This classification was perpetuated by Biström (1988b). Most recently, *Neobidessodes* Hendrich and Balke was erected to include the Australian species placed in *Bidessodes* (Hendrich *et al.*, 2009), thereby restricting the genus to include only Neotropical species.

Diversity. After rearrangements the genus includes 16 species. They were revised by Young (1986b).

Natural History. Members of this group are found in lotic and shallow lentic habitats. Some species appear to be relatively rare, but others can be very common, particularly in sandy streams with detritus. They often come to lights, though generally not in large numbers.

Distribution. This genus is found in lowland South America (Map 37.6) with most species in the north.



Map 37.6. Distribution of *Bidessodes*.

Genus *Bidessonotus* Régimbart, 1895

Body Length. 1.3–2.4mm.

Diagnosis. Among Bidessini genera, *Bidessonotus* is distinguishable based on the combination of (Fig. 37.51): (1) the transverse occipital line present; (2) the anterior clypeal margin unmodified; (3) the basal elytral stria present; (4) the basal pronotal striae

Fig. 37.51. *Bidessonotus obtusatus.* Scale = 1.0mm.

present; (5) the elytral sutural stria absent; and (6) the pro- and mesotarsi more distinctly pentamerous than in other hydroporines, though protarsomere IV is relatively short (Fig. 37.31a). Males and females are conspicuously sexually dimorphic. Females are dorsally microreticulate and often iridescent. Males have the metaventrite and medial portions of the metacoxae more strongly concave (Fig. 37.32a) and the mesotibiae more strongly curved (Fig. 37.33a) than in females. Finally, the male median lobe is bilaterally distinctly asymmetrical, which is uncommon in the Hydroporinae and secondarily derived.

Classification. Relationships with other genera are uncertain.

Diversity. There are currently 30 species assigned to *Bidessonotus*. Most of the species were revised first by J. Balfour-Browne (1947a) and more recently by Young (1990c).

Natural History. Specimens are generally found in ponds, forest pools, and streams with considerable vegetation or detritus. They often come to lights in numbers. The modifications to the male, concave ventral surface and curved mesotibia suggest some functional association with mating, but mating behavior has not been described for any member of the genus.

Distribution. This group occurs from southeastern Canada south through the eastern United States, south through lowland Mexico, the Caribbean and Central America, and throughout lowland South America (Map 37.7).

Map 37.7. Distribution of *Bidessonotus*.

Genus *Bidessus* Sharp, 1882

Body Length. 1.3–2.3mm.

Diagnosis. *Bidessus* is characterized among Bidessini by the following (Figs. 37.36a,52): (1) the transverse occipital line present; (2) the anterior clypeal margin unmodified; (3) the basal elytral stria present; (4) the basal pronotal striae present; (5) the elytral sutural stria present, though often indistinct posteriorly; (6) the male lateral lobes two-segmented; and (7) the transverse carina across the epipleuron at the humeral angle absent. Members of the genus are variable but often small and dorsally maculate or fasciate (Fig. 37.52)

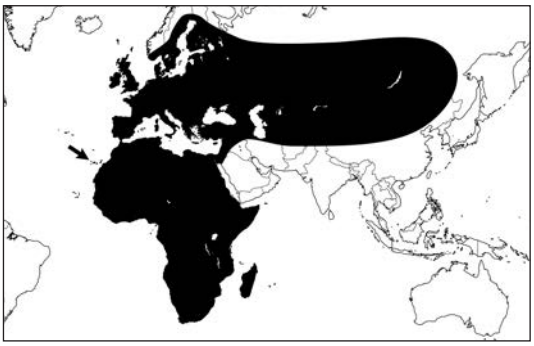
Classification. This was the original genus in the tribe, and many species now placed in other genera were originally placed in *Bidessus* by Sharp (1882) or subsequently described in this group by other authors. Currently, the genus is considerably more restricted in its circumscription.

Diversity. The genus still includes 50 species, which are diverse in body form. Most of the group was treated fairly recently by Biström (1983a; b; 1984a; 1985a; b; 1988a; b), Biström and Sanfilippo (1986), Biström and Nilsson (1990), and Fery (1991).

Fig. 37.52. *Bidessus toumodiensis.* Scale = 1.0mm.

Natural History. Species occur in many habitats from temporary pools to ponds, lakes and stream margins. Larvae were described by Nilsson (1985).

Distribution. As currently defined, this genus occurs in Europe, Africa, and eastward to China, Mongolia, and east Siberia (Map 37.8).



Map 37.8. Distribution of *Bidessus*.

Genus *Borneodessus* Balke, Hendrich, Mazzoldi, and Biström, 2002

Body Length. 2.8–3.5mm.

Diagnosis. This genus is characterized among Bidessini by the following (Figs. 37.13a,53): (1) the transverse occipital line absent; (2) the anterior clypeal margin angulate and margined, at least in the male; (3) the basal elytral stria absent; (4) the basal pronotal striae present; (5) the elytral sutural stria absent; (6) the male lateral lobes two-segmented; (7) a transverse carina across the epipleuron at the humeral angle absent; and (8) the prosternal process not excavated or margined. Specimens are robust, posteriorly somewhat attenuated, and mottled (Fig. 37.53).

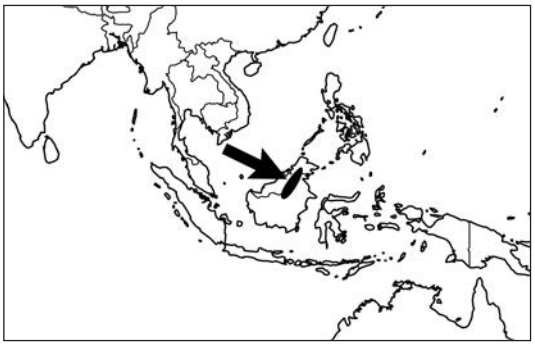
Fig. 37.53. *Borneodessus zetteli kalmantanensis.* Scale = 1.0mm.

Classification. Balke *et al.* (2002a) speculated that the most likely closest relative of *Borneodessus* was African *Clypeodytes*.

Diversity. There is only one species in this genus, *B. zetteli* Balke, Hendrich, Mazzoldi, and Biström, with two valid subspecies.

Natural History. Specimens were collected "among mats of floating roots and in small isolated puddles, at the edges of streams" (Balke *et al.*, 2002a).

Distribution. The single species is only known from Borneo (Map 37.9).



Map 37.9. Distribution of *Borneodessus*.

Genus *Brachyvatus* Zimmermann, 1919

Body Length. 1.3–1.7mm.

Diagnosis. This genus is characterized among Bidessini by the following (Figs. 37.41a,54): (1) the head with a distinct transverse occipital line between the posterior margins of the eyes; (2) the anterior clypeal margin modified, anteriorly with two distinctive tubercles medially; (3) the epipleuron with a transverse carina at the humeral angle; (4) the pronotum with the basal striae present and quite short; and (5) the elytron without a basal stria. Specimens are very small, robust and posteriorly attenuate, and dorsally concolorous (Fig. 37.54).

Classification. The genus appears to be closely related to *Hemibidessus* (Miller, 2001e).

Diversity. There are four valid species currently in this genus, but the group has never been comprehensively revised.

Natural History. Little has been documented about

Fig. 37.54. *Brachyvatus acuminatus*. Scale = 1.0mm.

Fig. 37.55. *Clypeodytes migrator*. Scale = 1.0mm.

Brachyvatus natural history. Young (1954) collected specimens in a variety of permanent habitats and at light. Large series of specimens can be collected at lights.

Distribution. *Brachyvatus* are found in lowland Central and South America south to Argentina and the Antilles with one species found north to Florida (Map 37.10). Since the group has not been revised, its distribution has never been well documented.

Map 37.10. Distribution of *Brachyvatus*.

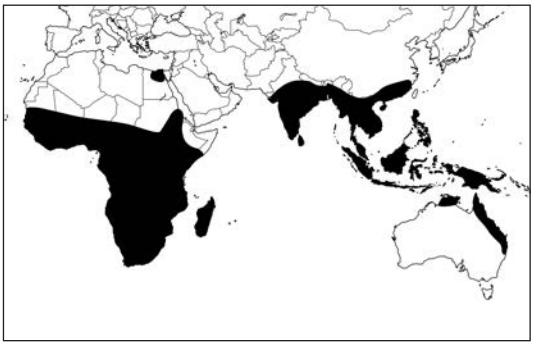
Genus *Clypeodytes* Régimbart, 1894

Body Length. 1.5–2.5mm.

Diagnosis. *Clypeodytes* differ from other Bidessini by the combination of (Fig. 37.55): (1) the transverse occipital line present; (2) the anterior clypeal margin modified, with a distinct flattened margin; (3) the basal pronotal striae present; (4) a basal elytral stria present in most species; (5) an elytral sutural stria absent; (6) the elytron with a low carina laterally in most species; (7) the epipleuron with a transverse carina at the humeral angle (Fig. 37.28a); (8) the lateral lobes of the aedeagus two-segmented; (9) most with the metaventrite with a line of punctures on each side (as in Fig. 37.28c); and (10) overall the body usually short and robust (Fig. 37.55). Members of *Clypeodytes* (*Hypoclypeus*) lack elytral striae and lines of punctures on the metaventrite. Members of the poorly known *C.* (*Paraclypeus*) *hemani* Vazirani lack carinae on the elytra.

Classification. This genus currently includes three subgenera: *Clypeodytes s. str.* is the largest, *C.* (*Hypoclypeus*) with four species, and *C.* (*Paraclypeus*) with one species. Not all the species in *Clypeodytes* are convincingly placed in the genus (Biström, 1988b; Balke *et al.,* 2002a). *Leiodytes* was previously regarded as another subgenus of *Clypeodytes* until Biström (1988b) elevated it.

Diversity. The genus includes 39 species, but Balke *et al.* (2002a) believed some Oriental species should move to other genera. The African species were revised by Biström (1988e), the Indian species by Vazirani (1968), and the Australian species by Watts (1978) and Hendrich and Wang (2006).



Map 37.11. Distribution of *Clypeodytes*.

Natural History. *Clypeodytes* are found in many habitats from temporary pools to ponds and streams. Some have been found in hot springs and lentic habitats with mineral substrates (Biström, 1988e). They often come in numbers to lights.

Distribution. *Clypeodytes* is known from Africa and Europe across Asia to Southeast Asia and Australia (Map 37.11).

Genus *Comaldessus* Spangler and Barr, 1995

Body Length. 1.5mm.

Diagnosis. *Comaldessus* are subterranean and, like many aquifer-inhabiting diving beetles, has characters typical of that lifestyle, including (Fig. 37.56): (1) depigmentation; (2) eyes absent; and (3) reduced swimming ability. From subterranean *Limbodessus* and *Trogloguignotus*, this group differs in the absence of metacoxal lines (Fig. 3.40b, like *Sinodytes*). From *Sinodytes*, *Comaldessus* differs in having a pair of distinctive basal striae (Fig. 37.56). Character states include (Fig. 37.56): (4) basal elytral stria present; (5) the basal pronotal striae present; (6) the anterior clypeal margin unmodified; and (7) a transverse carina across the elytral epipleuron at the humeral angle absent.

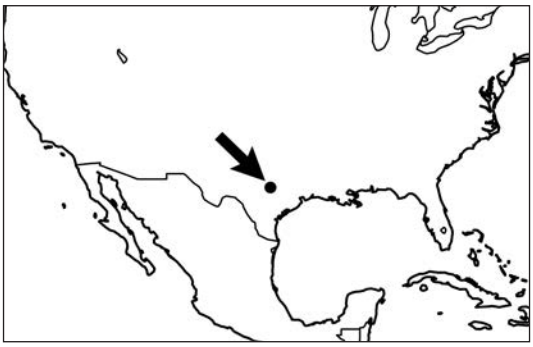
Classification. The genus has always been placed in Bidessini, but further relationships are unknown.

Diversity. A single species is placed in this genus, *C. stygius* Spangler and Barr.

Natural History. *Comaldessus stygius* is known only from Comal Springs in south-central Texas, USA. This spring arises from the Edwards-Trinity Aquifer, a subterranean karst system in limestone dating to the mid to late Cretaceous (Ryder, 1996). Another subterranean diving beetle is also known from this particular spring, *Haideoporus texanus* Young and Longley. Other subterranean diving beetles in the Edwards-Trinity Aquifer are *Ereboporus naturaconservatus* Miller, Gibson, and Alarie and *Psychopomporus felipi* Jean, Telles, and Miller.

Fig. 37.56. *Comaldessus stygius.* Scale = 1.0mm.

Distribution. The single species is known only from Comal Springs in central Texas, USA (Map 37.12).



Map 37.12. Distribution of *Comaldessus*.

Genus *Crinodessus* Miller, 1997

Body Length. 2.5–2.6mm.

Diagnosis. *Crinodessus* are diagnosed by the following character combination (Fig. 37.57): (1) a transverse occipital line present on the posterodorsal surface of the head that is distinctly separated from the posterior margins of the small eyes; (2) the anterior clypeal margin prominent but not margined or beaded; (3) a pair of basal pronotal striae present; (4) a basal elytral stria present; (5) the sutural stria absent on the elytron; (6) broad separation of the genal line from the ventral margin of the eye; (7) the apical segment of the male lateral lobe distinctly elongate; (8) dense microreticulation on the ventral surface consisting of minute, isodiametric cells; and (9) the lateral outline of the body distinctly discontinuous between the pronotum and elytra.

Classification. *Crinodessus* is similar to *Liodessus* and *Neoclypeodytes* (Miller 1997; 1999), but relationships between these taxa are not clear.

Diversity. There is a single species in the genus, *C. amyae* Miller.

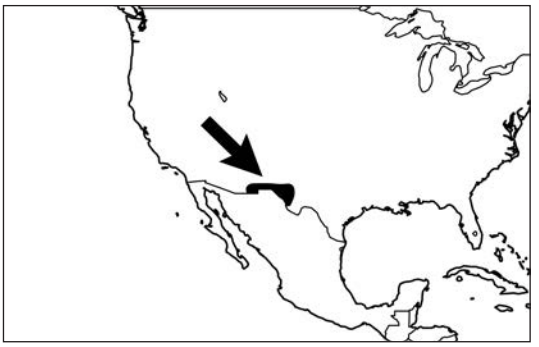
Natural History. *Crinodessus* have been collected from streams in semiarid to arid regions of the American Southwest. Miller (1999) suggested that

Fig. 37.57. *Crinodessus amyae*. Scale = 1.0mm.

Fig. 37.58. *Fontidessus toboganensis*. Scale = 1.0mm.

the body shape and reduced eyes might be correlated with hyporheic lifestyle in *Crinodessus*, but this has not be conclusively demonstrated. Little else is known about the biology of the single species.

Distribution. *Crinodessus amyae* is known from few localities in the southwestern United States (Map 37.13). Based on this distribution, it seems likely the species occurs farther south into Mexico as well.



Map 37.13. Distribution of *Crinodessus*.

Genus *Fontidessus* Miller and Spangler, 2008

Body Length. 1.1–1.6mm.

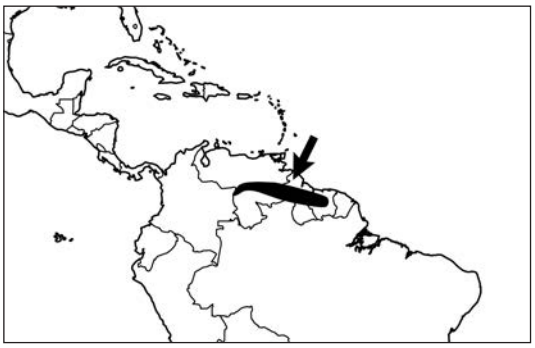
Diagnosis. *Fontidessus* differs from other Bidessini by the combination of (Figs. 37.13b,58): (1) a transverse occipital line absent on the head; (2) the anterior clypeal margin unmodified; (3) a pair of basal pronotal striae present; (4) the basal elytral stria absent; (5) the elytral sutural stria faintly present in some specimens; (6) the elytron without longitudinal carinae; (7) the epipleuron without a transverse carina at the humeral angle; (8) the lateral lobes of the male aedeagus two-segmented; (9) the habitus elongate and oval, with lateral pronotal and elytral margins nearly continuously and shallowly curved; and (10) the metatrochanter extremely large relative to the metafemur, approximately 0.6 × the length of the metafemur.

Classification. Miller and Spangler (2008) considered the genus similar to *Bidessodes* and *Uvarus*.

Diversity. There are currently seven species in this recently described genus. *Fontidessus* was originally described to include three species (Miller and Spangler, 2008) with four additional species described in a later paper (Miller and Montano, 2014).

Natural History. *Fontidessus* are hygropetric and found in thin layers of water at the edge of streams or in seepages on bare rock, where they live in cracks.

Distribution. Collectively these species are found along the margins of the Guyana Shield of northern South America from southern Venezuela east to Suriname (Map 37.14). The known distribution of each species is relatively small, and some species are known only from one or two sites.



Map 37.14. Distribution of *Fontidessus*.

Genus *Geodessus* Brancucci, 1979

Body Length. 1.4–1.6mm.

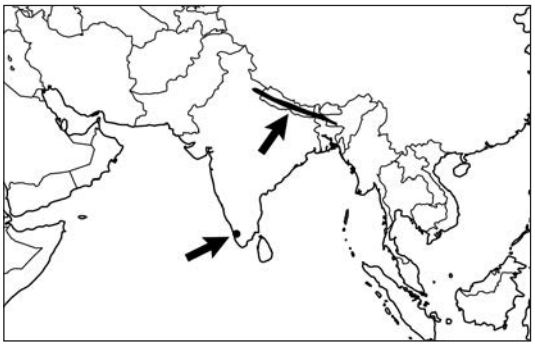
Diagnosis. The species in this genus are characterized by terrestrial habitat (living under leaf litter); the reduction of natatory setae on the mesotibia, metatibia, and metatarsi; and the presence of grooves on the lateral portion of each abdominal sternum. The genus is similar to terrestrial diving beetles in the genus *Paroster*, but they lack the lateral abdominal grooves. *Geodessus* is a bidessine, so it differs from terrestrial *Paroster* by the diagnostic features of the tribe. Specimens are small and robust (Fig. 37.59).

Classification. The relationships of *Geodessus* are ambiguous (Balke and Hendrich, 1996).

Diversity. There are two species, *G. besucheti* Brancucci and *G. kejvali* Balke and Hendrich. They were differentiated by Balke and Hendrich (1996).

Natural History. This is one of only a few seemingly terrestrial dytiscids (the others include the ambiguously classified *Typhlodessus* and two species of *Paroster*). The biology of *Geodessus* has been discussed by Brancucci (1979; 1980b; 1985a) and Balke and Hendrich (1996). Specimens have been collected by sifting forest litter, but specimens have also been collected from streams (Brancucci and Hendrich, 2010), suggesting they may be less terrestrial than previously reported. Larvae are unknown, and it is not known whether they are terrestrial.

Distribution. One of two known species is found in northern India and Nepal and the other is found in southern India (Map 37.15).



Map 37.15. Distribution of *Geodessus*.

Genus *Gibbidessus* Watts, 1978

Body Length. 2.0mm.

Diagnosis. *Gibbidessus* are characterized by the following (Fig. 37.60): (1) the head with a transverse occipital line present; (2) the anterior clypeal margin unmodified; (3) the pronotum with a pair of basal striae; (4) the elytron with a basal stria; (5) the elytron without sutural striae; (6) the epipleuron without a transverse carina at the humeral angle; (7) the body lateral outline relatively evenly curved between the pronotum and elytron; (8) the metacoxal lines short, separated by about their length (Fig. 37.34a); and (9) the male lateral lobe of the aedeagus two-segmented. Specimens are small and oval (Fig. 37.60).

Classification. Watts (1978) thought the genus might be related to *Clypeodytes* or Australian "*Liodessus*" (=*Limbodessus*). In molecular studies it has been resolved closest to Australian *Uvarus pictipes* (e.g., Balke and Ribera, 2004), but see under *Uvarus*.

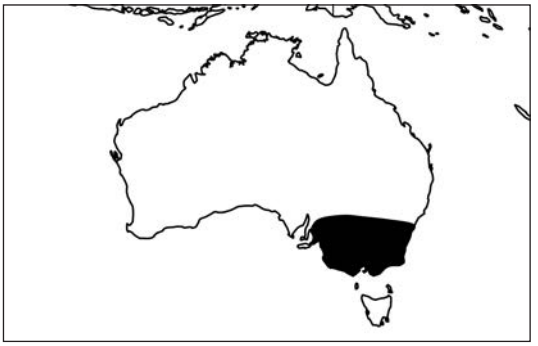
Fig. 37.59. *Geodessus kejvali*. Scale = 1.0mm.

Fig. 37.60. *Gibbidessus chipi*. Scale = 1.0mm.

Diversity. There is one *Gibidessus* species, *G. chipi* Watts.

Natural History. *Gibbidessus* specimens have been collected from shallow ponds with limited emergent vegetation. Little else is known of the species.

Distribution. The single species in this genus occurs in southeastern Australia (Map 37.16).



Map 37.16. Distribution of *Gibbidessus*.

Genus *Glareadessus* Wewalka and Biström, 1998

Body Length. 1.8–1.9mm.

Diagnosis. *Glareadessus* are characterized by the following (Figs. 37.16c,61): (1) the head without a transverse occipital line; (2) the anterior clyeal margin unmodified; (3) the pronotum with a pair of basal striae; (4) the elytron with a basal stria; (5) the elytron with a sutural stria but without longitudinal keels; (6) the epipleuron without a transverse carina at the humeral angle; (7) the lateral outline distinctly discontinuous between the pronotum and elytron; and (8) males with a two-segmented lateral lobe. These species are very similar to those in *Hydroglyphus*, but that genus has three-segmented lateral lobes and tends to be more continuously curved between the pronotum and elytron.

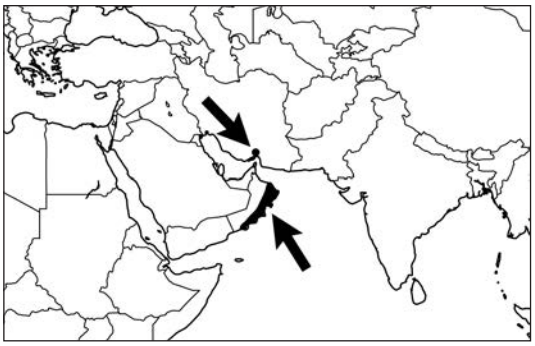
Fig. 37.61. *Glareadessus stocki.* Scale = 1.0mm.

Classification. *Glareadessus* is probably closely related to *Hydroglyphus*.

Diversity. There are two species in this genus, *G. franzi* Wewalka and Biström and *G. stocki* Wewalka and Biström, which were revised by Wewalka and Biström (1998).

Natural History. Species in this genus are found in rheophilic habitats in wadis and have been collected at lights (Wewalka and Bistrom, 1998). Larvae were described by Alarie and Wewalka (2001).

Distribution. *Glareadessus* are found in Oman, United Arab Emirates, and southern Iran (Map 37.17).



Map 37.17. Distribution of *Glareadessus*.

Genus *Hemibidessus* Zimmermann, 1921

Body Length. 2.2–3.4mm.

Diagnosis. *Hemibidessus* are diagnosable within Bidessini by the combination of (Figs. 37.41b,62): (1) the head with a distinct transverse occipital line between the posterior margins, or near the margins, of the eyes; (2) the anterior clypeal margin modified, anteriorly truncate and laterally thickened forming a bisinuate bead (less modified in *H. spiroductus* Miller than in other species); (3) the epipleuron with a transverse carina at the humeral angle; (4) the pronotum with basal striae present and short (very short in *H. spiroductus*); and (5) the elytron without a basal stria. Species in the group have members that are short and robust (Fig. 37.41b) to more elongate (Fig. 37.62), and from dorsally concolorous to maculate or fasciate (Fig. 37.62).

Fig. 37.62. *Hemibidessus bifasciatus.* Scale = 1.0mm.

Classification. *Hemibidessus* is closely related to *Brachyvatus* (Miller, 2001c; Miller and Bergsten, 2014a).

Diversity. There are currently six species assigned to *Hemibidessus*. The genus was revised by Miller (2001e).

Natural History. Young (1967a) found the species in both lentic and lotic habitats, but specimens are usually in lentic waters with dense vegetation (Miller, 2001b). They often come to lights.

Distribution. The species are found in lowland South America from Venezuela to northeastern Argentina (Map 37.18).

Map 37.18. Distribution of *Hemibidessus*.

Genus *Huxelhydrus* Sharp, 1882

Body Length. 2.8–3.0mm.

Diagnosis. *Huxelhydrus* are characterized within Bidessini by the following (Fig. 37.63): (1) the head without a transverse occipital line, the pronotum with a pair of basal striae; (2) the anterior clypeal margin unmodified; (3) the elytron with a basal stria but without a sutural stria; (4) the epipleuron without a transverse carina at the humeral angle; and (5) the elytron with two relatively distinct longitudinal series of punctures.

Fig. 37.63. *Huxelhydrus syntheticus.* Scale = 1.0mm. Photo courtesy of R. Leschen and B. Rhode, Landcare Research, Aukland, New Zealand. Used with permission.

Classification. The genus *Huxelhydrus* is clearly within the definition of Bidessini, but its relationships with other genera in the group are unknown.

Diversity. There is a single *Huxelhydrus* species, *H. syntheticus* Sharp.

Natural History. The species is known mainly from lotic habitats or, more rarely, ponds (Ordish, 1966).

Distribution. The single species in this genus is endemic to the North and South Islands of New Zealand (Map 37.19).

Map 37.19. Distribution of *Huxelhydrus*.

Genus *Hydrodessus* J. Balfour-Browne, 1953

Body Length. 1.5–4.1mm.

Diagnosis. Members of *Hydrodessus* lack most of the diagnostic features of other members of the tribe. Specimens do not have a transverse occipital line on the head, basal striae on the elytra or pronotum, sutural striae on the elytra, or a transverse carina on the epipleuron (Figs. 37.6a,64). The anterior clypeal margin is unmodified. The male lateral lobes are distinctly one-segmented. Most members of the group have the metaventrite with distinct longitudinal carinae extending from the metasternal process posteriorly along each side and often contiguous with the metacoxal lines, which also form carinae (Fig. 37.8b). Most specimens also have an elytral carina extending from the humeral angles posteriorly dorsad of the epipleural carina (Fig. 37.8a). The metasternal carinae are variable with some species strongly carinate, others with the carinae absent, and still others with a short carina. Similarly, the lateral elytral carinae in some species are very long, well marked, and extend well beyond the middle of the elytra, but in other species this carina is short or indistinct, and in others it is absent. A few species lack both features but appear to be related to the other members of the group based on general similarity. As such, this genus is currently difficult to diagnose based on discrete characters.

Classification. *Hydrodessus* was historically placed in Bidessini (Young, 1967a; 1969) but removed from the tribe after Biström (1988b) defined the tribe based on bisegmented male lateral lobes, which are one-segmented in *Hydrodessus*. However, at least some species have a distinct spermathecal spine and five-lobed proventricular teeth, characteristic of Bidessini as defined by Miller (2001c), and the genus was placed back in that tribe by Miller and Bergsten (2014a). They are related to *Peschetius* and *Amarodytes* (Miller and Bergsten, 2014a).

Diversity. At present the genus includes 30 described species which were revised by Miller (in press).

Natural History. Specimens of *Hydrodessus* are quite rare in collections. They are rarely collected in series. They can be collected at lights and from forest streams. Little is known of their natural history.

Distribution. *Hydrodessus* occur in northern South America throughout the Guiana Shield south to Paraguay and southern Brazil (Map 37.20).

Map 37.20. Distribution of *Hydrodessus*.

Genus *Hydroglyphus* Motschulsky, 1853

Body Length. 1.4–3.4mm.

Diagnosis. *Hydroglyphus* are characterized by the following (Figs. 37.16a,65): (1) the head without a transverse occipital line; (2) the anterior clypeal

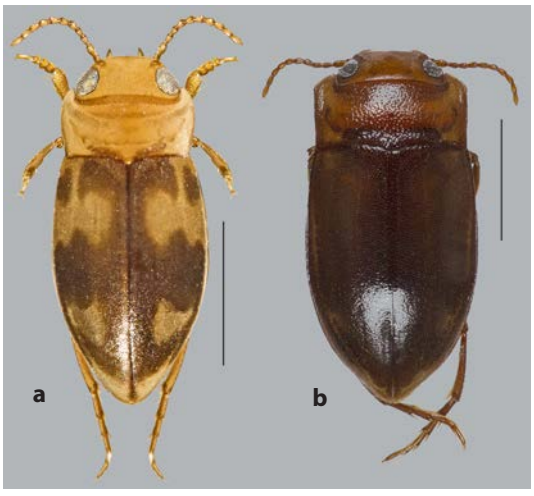


Fig. 37.64. *Hydrodessus* species. **a**, *Hydrodessus surinamensis*. **b**, *H. angularis*. Scale = 1.0mm.

Fig. 37.65. *Hydroglyphus daemeli.* Scale = 1.0mm.

margin unmodified; (3) the pronotum with a pair of basal striae; (4) the elytron with a basal stria and distinctive sutural stria; (5) the epipleuron without a transverse carina at humeral angle; (6) the body form elongate with the lateral outline approximately continuous between the pronotum and elytron; and (7) a three-segmented lateral lobe present in males. *Hydroglyphus* are similar to *Glareadessus*, but that genus has two-segmented lateral lobes and a more discontinuous lateral outline (Fig. 37.61). Many of the species in *Hydroglyphus* are dorsally fasciate or maculate (Fig. 37.65).

Classification. Many *Hydroglyphus* were historically described under the genus name *Guignotus* Houlbert, a junior synonym of *Hydroglyphus* (Biström and Silfverberg, 1981). The group was treated in Africa, where most of the species occur, by Biström (1986c), in Australia by Watts (1978) and Hendrich (1999), in India by Vazirani (1968), and in Europe by Guignot (1933), Franciscolo (1979a), Nilsson and Holmen (1995), and Zaitzev (1953).

Diversity. This is a large, species-rich group with currently 89 valid species.

Natural History. *Hydroglyphus* are found in many habitats, including temporary or seasonal pools, ponds, lake margins, cattle holes and animal watering tanks, and slow streams or stream margins, often in areas with mineral substrates. Some are characteristic of saline habitats. They are often quite abundant and readily come to lights, often in large numbers.

Distribution. *Hydroglyphus* are found throughout Africa, much of Europe, and southern Asia south to Australia (Map 37.21).

Map 37.21. Distribution of *Hydroglyphus*.

Genus *Hypodessus* Guignot, 1939

Body Length. 2.0–3.1mm.

Diagnosis. *Hypodessus* are characterized by the following (Fig. 37.66): (1) the head without a transverse occipital line; (2) the anterior clypeal margin unmodified; (3) the pronotum without basal striae or with these represented by only a few indistinct punctures; (4) the elytron without a basal stria, sutural stria, or longitudinal carinae; (5) the epipleuron without a transverse carina at the humeral angle; (6) the body form robust with the lateral outline approximately continuous between the pronotum and elytron; and (7) the male lateral lobe of the aedeagus two-segmented. Species in this group range from evenly pale to distinctly fasciate or maculate.

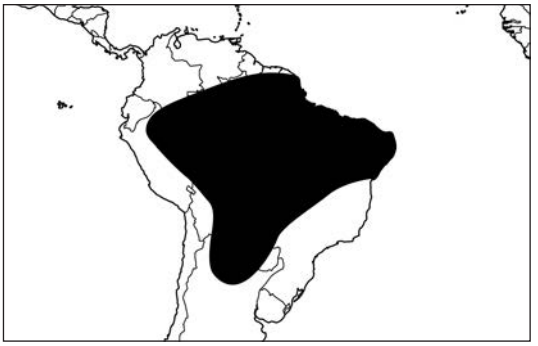
Classification. It is unknown if the genus is monophyletic or what its relationships are to other genera.

Diversity. *Hypodessus* includes six species, but the group has not been revised in modern times.

Natural History. Little is known about the natural history of this group. Specimens have been found in the margins of streams and at lights.

Fig. 37.66. *Hypodessus* sp. Scale = 1.0mm.

Distribution. This group is found in lowland South America (Map 37.22).



Map 37.22. Distribution of *Hypodessus*.

Genus *Incomptodessus* Miller and García, 2011

Body Length. 1.3–1.5mm.

Diagnosis. *Incomptodessus* differs from others in the tribe by the combination of (Figs. 37.6c,67): (1) a transverse occipital line present; (2) the anterior clypeal margin unmodified; (3) a pair of basal pronotal striae present; (4) the basal elytral stria and sutural stria absent; (5) the elytron without longitudinal carinae; (6) the epipleuron without a transverse carina at the humeral angle; (7) the lateral lobes of the male aedeagus two-segmented; (8) the body shape elongate, the lateral margin moderately discontinuous between the pronotum and elytron; (9) the lateral pronotal bead narrow; and (10) the metaventrite and metacoxae impunctate (Fig. 37.44b).

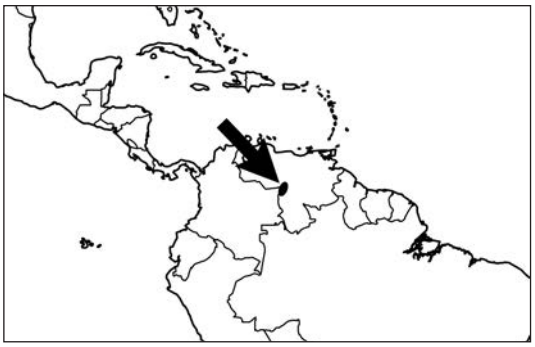
Fig. 37.67. *Incomptodessus camachoi*. Scale = 1.0mm.

Classification. Relationships of *Incomptodessus* are unclear (Miller and Garcia, 2011).

Diversity. There is a single species in this recently described genus, *I. camachoi* Miller and García.

Natural History. *Incomptodessus camachoi* is hygropetric and found in shallow rock pools, seeps, and stream margins on inselbergs (granite outcrops), sometimes found in huge numbers.

Distribution. *Incomptodessus camachoi* is found only in a small area where the Orinoco flows around the Guiana Shield (Map 37.23).



Map 37.23. Distribution of *Incomptodessus*.

Genus *Kakadudessus* Hendrich and Balke, 2009

Body Length. 2.2–2.3mm.

Diagnosis. *Kakadudessus* are characterized by the following character combination (Figs. 37.29b,68): (1) the body form is elongated, dorsoventrally compressed and flattened, and there are pale yellowish maculae on the elytra; (2) the head has a transverse occipital line; (3) the anterior clypeal margin is bordered; (4) the pronotum has a pair of basal stria; (5) the elytron has a basal stria; (6) the elytron does not have carinae, a sutural stria or accessory striae; (7) the elytral epipleuron does not have a transverse carina at the humeral angle; (8) the prosternal process is elongate and slender and reaches the metaventrite; (9) the metaventrite has rows of punctures at the midline; (10) the metacoxal lines are longer than the distance between them and strongly diverge anteriorly; and (11) the male lateral lobes are two-segmented, slender, elongate, and bifid anteriorly.

Classification. Hendrich and Balke (2009) found the species to possibly be near *Uvarus* or *Gibbidessus*, though *Kakadudessus* has a transverse occipital line.

Diversity. There is a single species in this genus, *K.*

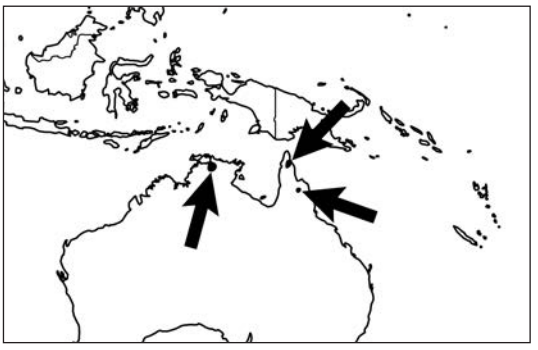
Fig. 37.68. *Kakadudessus tomweiri.* Scale = 1.0mm.

Fig. 37.69. *Leiodytes evanescens.* Scale = 1.0mm.

tomweiri Hendrich and Balke.

Natural History. Specimens are not common at sites where they occur, which are pools in otherwise dry riverbeds with sand or mud and leaves as substrate (Hendrich and Balke, 2009). Hendrich and Balke (2009) provide additional details of associations with other diving beetle species.

Distribution. *Kakadudessus* are known from northern Australia (Map 37.24).



Map 37.24. Distribution of *Kakadudessus*.

Genus *Leiodytes* Guignot, 1936

Body Length. 1.4–2.2mm.

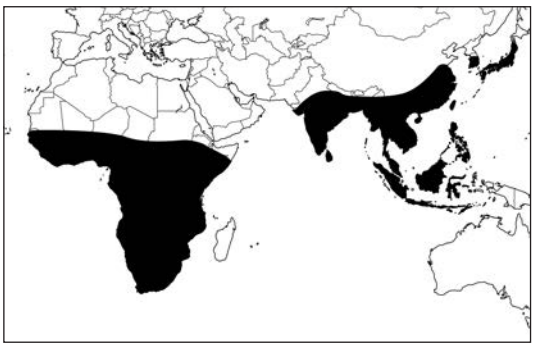
Diagnosis. *Leiodytes* differs from other Bidessini by the combination of (Fig. 37.69): (1) a transverse occipital line present; (2) the anterior clypeal margin modified or not; (3) a pair of basal pronotal striae present; (4) basal striae present but sutural striae absent on the elytron; (5) the elytron lacks carinae; (6) the epipleuron does not have a transverse carina at the humeral angle; (7) the lateral lobes of the male aedeagus are two-segmented; (8) the body shape is variable, robust to elongate; and (9) the metaventrite with a line of punctures on each side (Fig. 37.28c).

Classification. This was considered a subgenus of *Clypeodytes* until Biström (1988b) elevated it.

Diversity. There are currently 27 species in the group. The African species were treated by Biström (1987b; 1993) and the Indian ones by Vazirani (1968).

Natural History. Specimens are often found in pools and streams with mineral substrates and they come to lights. Little is known about their biology.

Distribution. Species are found in Africa, India, Japan, and Southeast Asia (Map 37.25).



Map 37.25. Distribution of *Leiodytes*.

Genus *Limbodessus* Guignot, 1939

Body Length. 0.9–4.8mm.

Fig. 37.70. *Limbodessus* species. **a**, *L. compactus.* **b**, *L. inornatus.* **c**, *L. macrolornaensis*. **d**, *L. macrotarsus.* Scales = 1.0mm. Photos c and d thanks to C. H. S. Watts and H. Hamon, South Australia Museum, Adelaide, Australia. Used with permission.

Diagnosis. One common epigean species, *L. compactus* (Clark), is characterized in Bidessini by (Fig. 37.70): (1) absence of a transverse occipital line across the head; (2) presence of a transverse carina across the elytral epipleuron at the humeral angle; (3) the anterior clypeal margin not modified; (4) the pronotum with a pair of basal striae; and (5) the elytron with a basal stria but without a sutural stria or longitudinal carinae. Several additional epigean species (transferred into the genus recently) instead lack the transverse carina across the elytral epipleuron at the humeral angle; have a distinct, faint, or partly obsolete tranvserse occipital line; and may lack elytral striae (Fig. 37.70b).

To further complicate diagnosis of this genus, most species of *Limbodessus* are subterranean with typical characteristics of this habitat, including depigmentation, reduction or loss of eyes, cordate pronota, and flightlessness (Fig. 37.70c,d) They do not have a transverse epipleural carina nor a transverse occipital line. They are otherwise rather variable in characters associated with Bidessini. From *Sinodytes* and *Comaldessus*, the subterranean and hyporheic *Limbodessus* can be distinguished by the presence of distinctive metacoxal lines. Given the diversity of these *Limbodessus*, the group is not easily diagnosable from another subterranean taxon using external characters, *Trogloguignotus*, from Venezuela.

The only known consistently diagnostic character in *Limbodessus* appears to be the broad male lateral lobes with a distinctive apical hook-shaped lobe (Fig. 37.38), but this requires dissection and is somewhat modified in certain taxa.

Classification. Historically one widespread species, *L. compactus* and its synonyms, was recognized in this genus. *Limbodessus* now includes a great number of subterranean and hyporheic Bidessini from Australia. Several genera based on subterranean or hyporheic forms are now regarded as junior synonyms of *Limbodessus,* including *Boongurrus* Larson, *Kintingka* Watts and Humphreys, *Nirridessus* Watts and Humphreys, and *Tjirtudessus* Watts and Humphreys, with these conclusions based largely on recent molecular analyses (Balke and Ribera 2004) and the common presence of a uniquely shaped male lateral lobe (Fig. 37.38). In addition to *L. compactus*, there are also now additional epigean species in the genus transferred from *Liodessus* by Balke and Ribera (2004) based also mainly on molecular analysis and the male lateral lobe character (Fig. 37.38).

Diversity. Currently there are 76 valid species in *Limbodessus*. Most of the known species were keyed or diagnosed by Watts and Humphreys (2006; 2009). The epigean species were revised by Watts and Leys (2005).

Natural History. The epigean *Limbodessus* occur in ponds and streams. The other species are hyporheic or subterranean in Australia with many of them occurring in paleodrainages in arid Western Australia. This habitat and the evolution of the diving beetles therein are reviewed by Leys *et al.* (2003) and Leys and Watts (2008).

Distribution. Most *Limbodessus* are found in Australia with one species, *L. compactus*, found from Japan south through Southeast Asia and Australia to several Pacific islands (Map 37.26). Balke *et al*. (2015) recently described a couple of microendemic epigean species from Indonesian New Guinea.

Map 37.26. Distribution of *Limbodessus*.

Genus *Liodessus* Guignot, 1939

Body Length. 1.2–3.0mm.

Diagnosis. *Liodessus* can be distinguished within Bidessini by the following character combination (Figs. 37.16b,71): (1) a transverse occipital line is present between the posterior margin of the eyes; (2) the anterior clypeal margin is simple, not beaded or modified; (3) the pro- and mesotarsi are pseudotetramerous with tarsomere IV small and obscured in the ventral lobes of tarsomere III; (4) the basal pronotal and elytral striae are well developed (a couple of unusual species have the elytral striae reduced or absent); (5) an oblique carina on the elytral epipleuron at the humeral angle absent; (6) the metasternum simple; (7) the elytron without a sutural stria (a couple of species have a linear series of punctures on each side of the elytral suture); (8) the elytron without an accessory stria or linear series of punctures basally between the elytral stria and suture; and (9) abdominal sternum six narrow and triangular andv with moderately distinct basolateral impressions.

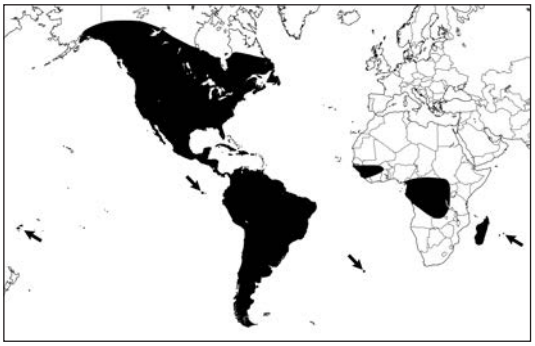
Fig. 37.71. *Liodessus affinis.* Scale = 1.0mm.

Classification. This is a problematic group. Among the Bidessini there are, historically and superficially, two main groups, those with an occipital line and those without. Among those with a transverse occipital line, there are numerous genera with distinctive feature and character combinations. Those species that are relatively generalized, however, have been placed in *Liodessus*, though it is by no means evident that the genus is monophyletic. Gradually, such as with the Australian fauna, the species have been transferred to other genera (Balke and Ribera, 2004; Nilsson and Fery 2006; Balke *et al*., 2015).

Diversity. There are today 37 species in *Liodessus*, including one on Fiji. The Nearctic species were treated by Miller (1998) and Larson and Roughley (1990), the African ones by Biström (1988c), but the Central and South American species have not been treated since Sharp's (1882) monograph.

Natural History. *Liodessus* can be found in a variety of habitats, but often on mineral substrates at the margins of lentic habitats. Specimens are also often found at the margins of marshes with considerable emergent vegetation, streams, rock pools, and even relatively deep waters (Young, 1954; Miller, 1998). Larvae have been described by Watts (1970), and variation in larval stemmata has been investigated by Shepley-James *et al.* (2009).

Distribution. Species currently assigned to *Liodessus* are found in North and South America, Africa, and Fiji (Map 37.27).



Map 37.27. Distribution of *Liodessus*.

Genus *Microdessus* Young, 1967

Body Length. 1.5–1.8mm.

Diagnosis. *Microdessus* are characterized by the following character combination (Fig. 37.72): (1) the

Fig. 37.72. *Microdessus atomarius.* Scale = 1.0mm.

Fig. 37.73. *Neobidessodes thoracicus.* Scale = 1.0mm.

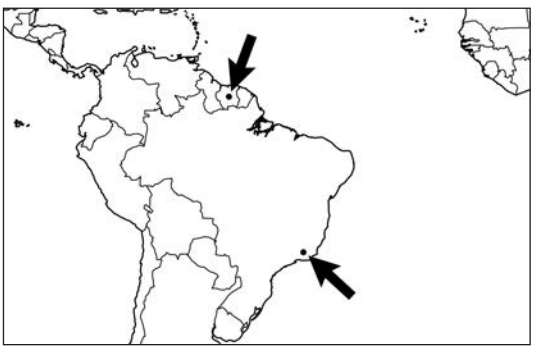
head without a transverse occipital line; (2) the anterior clypeal margin unmodified; (3) the pronotum with a pair of basal striae; (4) the elytron with a basal stria, but without a sutural stria; (5) the epipleuron without a transverse carina at the humeral angle; and (6) the male median lobe complex with four elongate apical rami. As its name suggests, members of *Microdessus* are very small, even for Bidessini (length < 1.0mm) .

Classification. Little has been written about the group except very general treatments by Young (1967a) and Biström (1988b). Young (1967a) stated that members of the genus have an occipital line, but they do not.

Diversity. There is a single species in the genus, *M. atomarius* (Sharp), originally described in *Bidessus*.

Natural History. Nothing is known about the biology of this species.

Distribution. *Microdessus atomarius* occurs in lowland South America (Fig. 37.28).



Map 37.28. Distribution of *Microdessus*.

Genus *Neobidessodes* Hendrich and Balke, 2009

Body Length. 1.3–4.2mm.

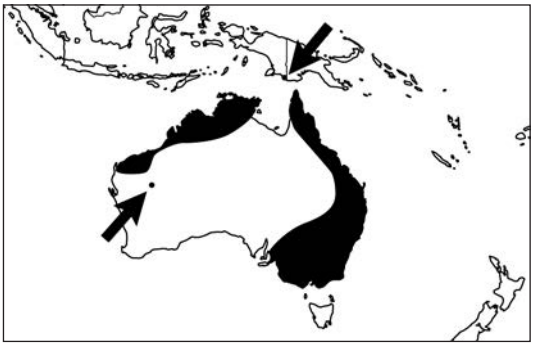
Diagnosis. *Neobidessodes* are diagnosable among Bidessini by the following (Figs. 37.13c,73): (1) the transverse occipital line is absent; (2) the anterior clypeal margin is unmodified; (3) the basal pronotal striae are present; (4) the basal elytral stria is absent; (5) the elytral sutural stria is absent; and (6) there is no transverse carina across the epipleuron at the humeral angle of the elytron. Members of this group are elongate oval and often dorsally longitudinally fasciate (Fig. 37.73). The group is very similar to *Bidessodes* but differs from that genus in lacking series of small denticles along the posterior margins of abdominal ventrites III–V (Fig. 37.14). There are two subterranean species with typical characteristics of that habitat, such as blindness and winglessness.

Classification. Species in *Neobidessodes* were, until recently, included in *Bidessodes*, a genus now restricted to the New World based on evidence that the two groups are not closely related (Hendrich *et al.*, 2009).

Diversity. There are currently 10 species in *Neobidessodes* revised in large part by Hendrich *et al.* (2009) with a subsequent new species described by Hendrich and Balke (2011). The two subterranean species were described by Watts and Humphreys (2003).

Natural History. The epigean species occur in sandy or gravelly streams, creeks, and pools associated with rivers (Hendrich *et al.,* 2009). Larvae were described by Michat *et al.* (2010).

Distribution. *Neobidessodes* are found in northern and eastern Australia and from southern New Guinea (West Papua) (Map 37.29). The two subterranean species are known from Western Australia.



Map 37.29. Distribution of *Neobidessodes*.

Genus *Neobidessus* Young, 1967

Body Length. 1.4–3.3mm.

Diagnosis. *Neobidessus* are characterized by the following character combination (Fig. 37.74): (1) the head with a transverse occipital line; (2) the anterior clypeal margin unmodified; (3) the pronotum with a pair of basal striae; (4) the elytron with a basal stria but without a sutural stria; (5) the elytron with an "accessory stria" between the basal stria and elytral suture, which is prominent on many specimens, but less distinct on others; (6) the epipleuron without a transverse carina at the humeral angle; and (7) the male median lobe and lateral lobes often asymmetrical. These beetles are generally elongate oval with longitudinal stripes on the elytron (Fig. 37.74).

Fig. 37.74. *Neobidessus woodruffi.* Scale = 1.0mm.

Classification. *Neobidessus* relationships with other genera are not known.

Diversity. This is a species-rich group of 29 valid species, revised in a two-part work by Young (1977; 1981d).

Natural History. *Neobidessus* are common in many lentic habitats from larger marshes with extensive vegetation to sandy pools. Less frequently they are found in the margins of streams. They often occur in huge numbers, and they often come to lights.

Distribution. Species in the group occur in the southeastern United States south through Mexico, Central America, and the Caribbean and throughout lowland South America (Map 37.30).

Map 37.30. Distribution of *Neobidessus*.

Genus *Neoclypeodytes* Young, 1967

Body Length. 1.6–2.5mm.

Diagnosis. *Neoclypeodytes* can be diagnosed by the following character combination (Fig. 37.75): (1) the head with a distinct transverse occipital line between the posterior margins, or near the margins, of the eyes; (2) the anterior clypeal margin anteriorly produced, strongly to slightly flattened with a medial, continuous, transverse bead or groove; (3) a basal elytral stria present; (4) a pair of basal pronotal striae present; (5) each elytron marked with two macula (reduced or otherwise modified depending on the species); and (6) a transverse elytral epipleural carina at the humeral angle present or absent. Some species (e.g., *N. plicipennis* (Crotch) and *N. leachi* (Leech)) have distinct longitudinal tectiform ridges, though these are not as strongly carinate as in, for example, *Anodocheilus*, *Yola,* or *Yolina*. Other species, such as *N. fryii* (Clark) and *N. tumulus* Miller have moderately distinct lateral tectiform ridges on the elytra.

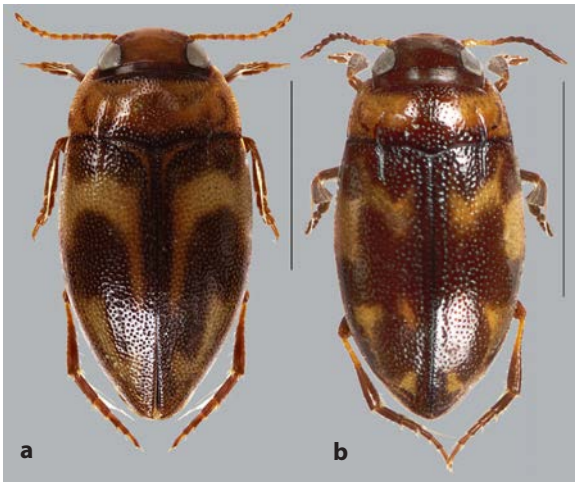


Fig. 37.75. *Neoclypeodytes* species. **a**, *N. cinctellus*. **b**, *N. ornatellus*. Scale = 1.0mm.

Classification. Like most bidessine genera, relationships between this genus and others in the tribe are ambiguous, and numerous affinities have been proposed, including *Anodocheilus*, *Bidessus,* or *Clypeodytes* (Young, 1967a) or *Bidessus*, *Leiodytes*, and *Platydytes* (Biström, 1988b) or *Clypeodytes*, *Platydytes,* and *Leiodytes* (Miller, 2001d).

Diversity. There are currently 27 species in the genus after a revision by Miller (2001d).

Natural History. Most species of *Neoclypeodytes* can be found in streams, rock pools, or similar habitats with mineral substrates. They are most diverse and common in exposed streams in arid regions of the desert southwest of the Nearctic region. *Neoclypeodytes ornatellus* (Fall), exceptionally, is most common in lentic habitats with dense emergent vegetation.

Distribution. This is mainly a western Nearctic group with species from southwestern Canada south through the western United States and Mexico, and a few species extending farther south into Panama and one species in Jamaica (Map 37.31).

Map 37.31. Distribution of *Neoclypeodytes*.

Genus *Pachynectes* Régimbart, 1903

Body Length. 2.2–2.7mm.

Diagnosis. *Pachynectes* have the following character combination (Fig. 37.76): (1) the head has a transverse occipital line; (2) the anterior clypeal margin is unmodified; (3) the pronotum has a pair of basal striae; (4) the elytron has a basal striae, but has sutural stria represented only by longitudinal series of punctures; (5) the elytron has a distinct longitudinal, lateral keel, but does not have keels on the disc of the elytron or has only a low, indistinct keel; (6) the elytral epipleuron has an incomplete transverse carina at the humeral angle; and (7) the lateral surfaces of the metaventrite have distinct longitudinal carinae. These beetles are generally relatively robust

Fig. 37.76. *Pachynectes costulifer.* Scale = 1.0mm.

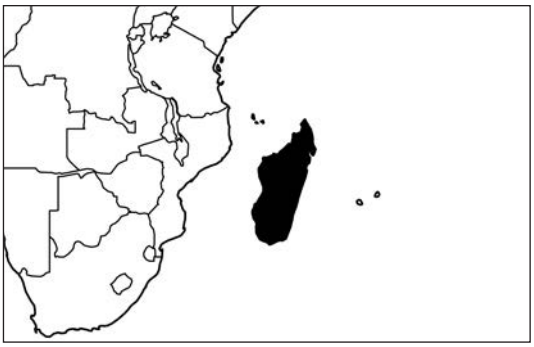
(Fig. 37.76). The two subgenera are characterized by a weak discal keel present on each elytron (*P.* (*Yoloides*) Guignot) or this keel absent (*Pachynectes s. str.*).

Classification. The genus, with two subgenera, *Pachynectes s. str.* and *P.* (*Yoloides*), was revised by Biström (1987c). Wang (2015) transferred the monotypic subgenus *Yoloides* to *Yolina*, but we retain it here since *Yoloides* is nested within the subgenus *Pachynectes* as presently defined (Bukontaite, 2015). However, *Pachynectes* and *Yolina* are probably closely related (Wang, 2015).

Diversity. Biström (1987c) recognized three species, but a number of new species have been discovered in recent years, and the genus is under treatment (Bergsten, in prep.). Their relationships with other Bidessini are unknown.

Natural History. *Pachynectes* are associated with running water, typically found in the margins of rocky or sandy streams and rivers or in rock pools associated to rivers.

Distribution. *Pachynectes* is restricted to Madagascar (Map 37.32).



Map 37.32. Distribution of *Pachynectes*.

Genus *Papuadessus* Balke, 2001

Body Length. 2.0–3.4mm.

Diagnosis. *Papuadessus* are Bidessini with (Fig. 37.77): (1) the transverse occipital line absent on the head; (2) the anterior clypeal margin unmodified; (3) the transverse carina across the elytral epipleuron at the humeral angle absent; (4) the basal elytral stria present; (5) the elytral sutural stria absent; (6) the elytron without rows of punctures; (7) the lateral lobes of the male aedeagus with two segments and apically simply rounded; and (8) the median lobe of the male aedeagus apically simple. Specimens

Fig. 37.77. *Papuadessus pakdjoko*. Scale = 1.0mm.

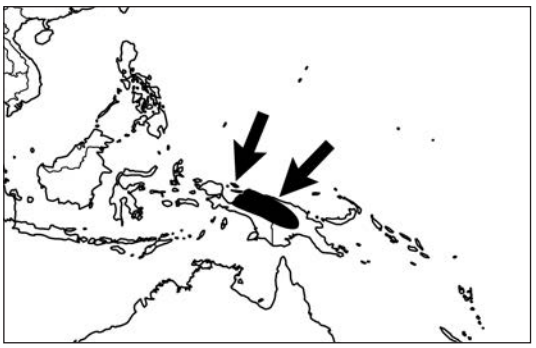
are darkly colored dorsally with fasciae (reduced in some specimens) .

Classification. The genus has unknown affinity with other Bidessini. The two species are not particularly similar but were placed together based especially on molecular data (Balke *et al.*, 2013b).

Diversity. There are two species in the genus, *P. pakdjoko* Balke and *P. baueri* Balke *et al.*

Natural History. Specimens of *P. baueri* were collected from a limestone sinkhole (Balke *et al.*, 2013b). Specimens of *P. pakdjoko* have been collected from medium to larger rivers, often with gravel substrate (Balke, 2001b; Balke *et al.,* 2013b).

Distribution. *Papuadessus* are known only from New Guinea (Map 37.33).



Map 37.33. Distribution of *Papuadessus*.

Genus *Peschetius* Guignot, 1942

Body Length. 2.9–4.4mm.

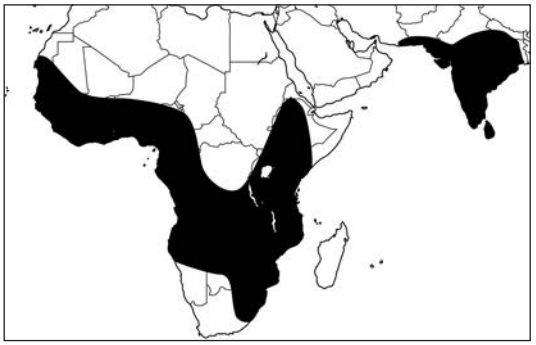
Diagnosis. The diagnostic morphology of *Peschetius* is unusual within all Dytiscidae in several respects, including (Figs. 37.7a,78): (1) presence of a deeply foveate region between the metacoxal lines; (2) a tectiform abdomen; (3) a broad elytral epipleuron; (4) conspicuous basal abdominal punctation; and (5) a strongly bicarinate elytral surface. These species are larger and morphologically more distinctive than many Bidessini genera. Most species are dorsally maculate and quite robust (Fig. 37.78).

Classification. *Peschetius* has had a contentious recent history of classification. Historically the genus was placed in the Hydroporini, regarded as possibly near the *Deronectes* group of genera (Régimbart, 1899; Zimmermann 1919; 1920), or perhaps near the Australian representatives of Hydroporini (Guignot, 1935; 1959b; J. Balfour-Browne, 1946). In a recent analysis, Miller *et al.* (2006) discovered that the genus has two characters that definitively place the group with Bidessini, the presence of a prominent internal spermathecal spine (Fig. 37.1) and a distinctly five-lobed transverse tooth of the proventriculus (Fig. 37.2). Historically Bidessini was defined using the two- or three-segmented lateral lobes (Biström, 1988b), but *Peschetius* is clearly associated with other members of this tribe based on these features, and Miller *et al.* (2006) expanded the definition of the tribe to include this genus. In a recent analysis, morphological and molecular data placed the genus together in a clade with *Amarodytes* and *Hydrodessus,* which are together sister to all other Bidessini (Miller and Bergsten, 2014a).

Diversity. There are 10 species in the genus that were recently revised by Biström and Nilsson (2003).

Natural History. Members of *Peschetius* are typically found in sandy streams, including weedy pools and streams with high gradients. They are more rarely collected in lentic habitats. They occasionally come to lights, and some are known from geothermally heated springs.

Distribution. *Peschetius* occur in sub-Saharan Africa, Iran, India, Sri Lanka, Pakistan, and Nepal (Map 37.34).



Map 37.34. Distribution of *Peschetius*.

Genus *Petrodessus* Miller, 2012

Body Length. 1.5–1.7mm.

Diagnosis. This genus differs from other Bidessini by the combination of (Figs. 37.4a,79): (1) the transverse occipital line absent; (2) a pair of basal pronotal striae present, basally deeply impressed with a shallow, transverse groove between them; (3) the basal elytral stria present, short, basally deeply impressed; (4) elytral sutural stria and carinae absent; (5) anterior clypeal margin strongly flattened, anteriorly produced, with broad anterior margin; (6) the elytral epipleuron without a transverse carina at the

Fig. 37.78. *Peschetius quadricostatus.* Scale = 1.0mm.

Fig. 37.79. *Petrodessus conatus.* Scale = 1.0mm.

humeral angle; (7) the lateral lobes of the male aedeagus two-segmented; and (8) the protibia broadly triangular and heavily spinous. Individuals also have few natatory setae on the legs, which are robust and spinous. These beetles are robust, oval, and dorsally concolorous (Fig. 37.79).

Classification. *Petrodessus* has unknown relationships to other Bidessini.

Diversity. There is only one species in this genus, *P. conatus* Miller.

Natural History. This species is hygropetric, occurring along the margins of waterfalls in tropical coastal forests.

Distribution. *Petrodessus* is known from a limited region of northeastern Australia (Map 37.35).

Map 37.35. Distribution of *Petrodessus*.

Genus *Platydytes* Biström, 1988

Body Length. 1.8–2.4mm.

Diagnosis. *Platydytes* are diagnosed from other Bidessini by the following character combination (Fig. 37.80): (1) the head with a transverse occipital line; (2) the anterior clypeal margin finely bordered, sometimes indistinctly; (3) the pronotum with a pair of basal striae; (4) the elytron without a basal stria, sutural stria, or carinae; and (5) the elytral epipleuron without a transverse carina at the humeral angle (Fig. 37.42). These beetles are generally relatively elongate and dorsoventrally flattened (Fig. 37.80).

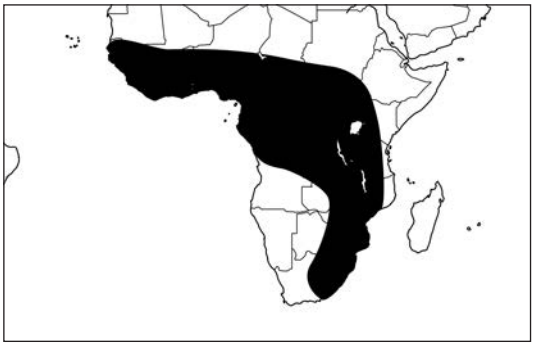
Fig. 37.80. *Platydytes coarctaticollis*. Scale = 1.0mm.

Classification. This genus was erected to include *P. coarctaticollis* (Régimbart) and *P. inspectatus* (Omer-Cooper), both formerly in *Clypeodytes*, and two additional new species, by Biström (1988b).

Diversity. There are four species in the genus. Biström (1988b) provided diagnoses for each species.

Natural History. At least some species have been found in small streams. Little else is known of the biology of the group.

Distribution. This group is found in sub-Saharan Africa (Map 37.36).



Map 37.36. Distribution of *Platydytes*.

Genus *Pseuduvarus* Biström, 1988

Body Length. 1.8–2.3mm.

Diagnosis. *Pseuduvarus* are characterized by the following character combination (Fig. 37.81): (1) the head without a transverse occipital line; (2) the anterior clypeal margin unmodified; (3) the pronotum with a pair of basal striae; (4) the elytron with a basal stria but without sutural striae, or only indistinct anteriorly; (5) the elytral epipleuron without a transverse carina at the humeral angle; (6) the body form elongate oval with the lateral outline approximately continuous between the pronotum and elytron; and (7) the lateral lobe of the male aedeagus three-segmented (Fig. 37.23a). This genus is diagnostically similar to *Hydroglyphus*, but that genus

Fig. 37.81. *Pseuduvarus vitticollis.* Scale = 1.0mm.

Fig. 37.82. *Sharphydrus coriaceus.* Scale = 1.0mm.

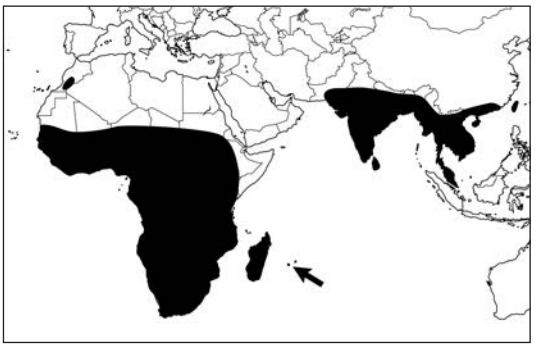
has a distinct sutural stria (Fig. 37.16a). The male median lobe of this species is strongly asymmetrical with apical spines directed ventrad.

Classification. This genus was erected to accommodate a single species, *P. vitticollis* (Boheman) (Biström, 1988b). The genus is probably closely related to *Hydroglyphus* and differs mainly in the lack of distinct sutural lines on elytra.

Diversity. There are two species in the genus, *P. vitticollis* and *P. secundus* Bilardo and Rocchi.

Natural History. The widespread genus is found in diverse habitats, including ponds and slow streams.

Distribution. *Pseuduvarus* is found throughout sub-Saharan Africa and Madagascar and Mauritius to areas of India and Southeast Asia (Map 37.37).



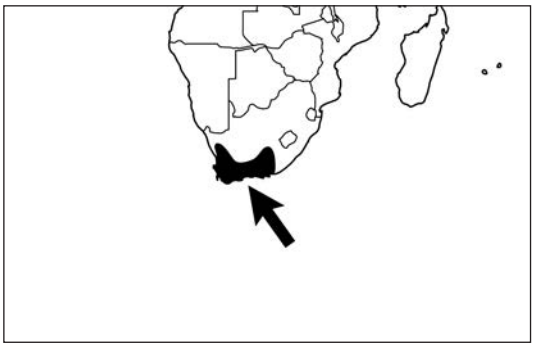
Map 37.37. Distribution of *Pseuduvarus*.

Genus *Sharphydrus* Omer-Cooper, 1958

Body Length. 2.3–3.0mm.

Diagnosis. *Sharphydrus* are separable from most other Bidessini by the following character combination (Fig. 37.82): (1) the head with a transverse occipital line; (2) the anterior clypeal margin unmodified; (3) the pronotum with a pair of basal striae; (4) the elytron without basal or sutural striae; (5) the elytron with (three species) or without (*S. coriaceus* (Régimbart)) longitudinal carinae (Fig. 37.24b); and (6) the epipleuron without a transverse carina at the humeral angle. The group is not well diagnosed relative to *Yola* (Bilton, 2013). Characteristics potentially separating most *Yola* from *Sharphydrus* include presence in the latter of coriaceous sculpturing on the dorsal surface, a weak groove on the anterior surface of the metaventrite (the groove deep in *Yola*), and only a discal carina present on the elytron (typically at least a discal and additional lateral carina present in *Yola*, and only a raised area present in some *Sharphydrus*). The most clear difference is the apex of the male median lobe which is trifid in *Sharphydrus* (Fig. 37.25a).

Classification. This genus includes two species previously placed in *Tyndallhydrus* and subsequently moved to *Sharphydrus* by Omer-Cooper (1958c).



Map 37.38. Distribution of *Sharphydrus*.

The two genera came out in a group together with *Yola* in the analysis by Ribera *et al.* (2008).

Diversity. There are now four known species. *Sharphydrus* was revised along with description of two new species by Bilton (2013).

Natural History. These species are found in pools in seasonal streams (Bilton, 2013).

Distribution. The species in this group are found only in southern South Africa (Map 37.38).

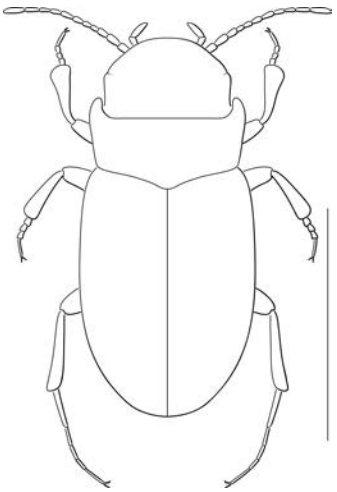
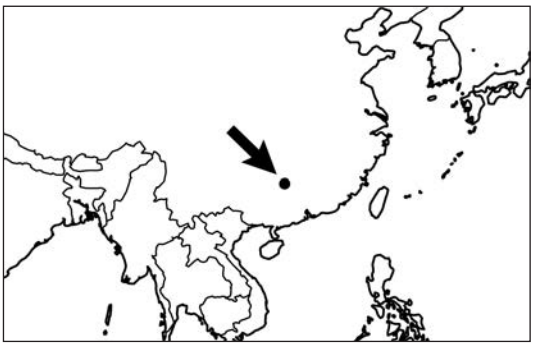


Fig. 37.83. *Sinodytes hubbardi* (drawn from Spangler, 1996). Scale = 1.0mm.

Genus *Sinodytes* Spangler, 1996

Body Length. 1.6–1.7mm.

Diagnosis. This subterranean bidessine is similar to *Comaldessus*, *Trogloguignotus,* and subterranean *Limbodessus* in having reduced eyes (absent in *Sinodytes*), reduced natatory setae, depigmentation, and other features associated with a subterranean lifestyle (Fig. 37.83). From these except *Comaldessus* it can be distinguished by the absence of metacoxal lines and absent pronotal striae (Fig. 37.83). *Sinodytes* have the pronotal striae absent (Fig. 37.83), whereas they are distinctive in *Comaldessus* (Fig. 37.56).



Map 37.39. Distribution of *Sinodytes*.

Classification. Spangler (1996) was uncertain of the tribal placement, but based on his estimation and examination of his images, the species is certainly likely to belong in this tribe. The holotype and single known specimen of this genus seem to be lost.

Diversity. There is one species in this genus, *S. hubbardi* Spangler, based on a single female specimen.

Natural History. The single specimen of this species was found in a calcareous rimstone pool in a cave (Spangler, 1996).

Distribution. *Sinodytes* are known only from Jiazhai Taiping Cave, Guangxi Province, Lingchuan County, China (Map 37.39).

Genus *Spanglerodessus* Miller and García, 2011

Body Length. 1.5–1.7mm.

Diagnosis. This genus differs from other bidessines by the combination of (Figs. 37.11b,84): (1) the transverse occipital line absent; (2) the anterior clypeal margin unmodified; (3) a pair of basal pronotal striae present; (4) the basal elytral stria absent; (5) an elytral sutural stria faintly present in some specimens; (6) the elytron without longitudinal carinae; (7) the epipleuron without a transverse carina at the humeral angle; (8) the lateral lobes of the male aedeagus two-segmented; (9) the body robust, short,

Fig. 37.84. *Spanglerodessus shorti.* Scale = 1.0mm.

with the lateral margins of the pronotum and elytron conspicuously rounded; and (10) the lateral bead on the pronotum prominently broad. Specimens do not have natatory setae on the legs, which are robust and spinous (Fig. 37.10a).

Classification. Relationships of this genus with other Bidessini are unknown.

Diversity. There is a single species in this recently described genus, *S. shorti* Miller and García.

Natural History. The single species in this genus is hygropetric, occurring along the margins of waterfalls (Miller and Garcia, 2011). Nothing else is known of its natural history.

Distribution. *Spanglerodessus* is known from few localities in Guyana and Venezuela (Map 37.40).

Map 37.40. Distribution of *Spanglerodessus*.

Genus *Tepuidessus* Spangler, 1981

Body Length. 1.8–2.2mm.

Diagnosis. This genus is characterized by the following character combination (Fig. 37.85): (1) the head does not have a transverse occipital line; (2) the anterior clypeal margin is unmodified; (3) the pronotum does not have basal striae but does have longitudinal depressions in the same areas; (4) the elytra do not have basal or sutural striae or carinae; (5) the elytral epipleuron does not have a transverse carina at the humeral angle; and (6) the body form is elongate with the lateral outline approximately continuous between the pronotum and elytron (Fig. 37.85). The last abdominal ventrite has a distinctive, deep groove continuous around the apical margin (Fig. 37.9b). Specimens are dorsally black in color (Fig. 37.85).

Classification. *Tepuidessus* relationships with all other Bidessini are currently unclear.

Fig. 37.85. *Tepuidessus breweri.* Scale = 1.0mm. Photo courtesy of L. Joly and M. Gaiani, Museo del Instituto de Zoologia Agricola, Universidad Central de Venezuela and used with permission.

Diversity. This genus includes a single species, *T. breweri* Spangler.

Natural History. The species is hygropetric with the type series collected in wet moss matts (Spangler, 1981a).

Distribution. *Tepuidessus* are known only from one locality in Venezuela (Map 37.41).

Map 37.41. Distribution of *Tepuidessus*.

Genus *Trogloguignotus* Sanfilippo, 1958

Body Length. 1.7–1.8mm.

Diagnosis. Among Bidessini, *Trogloguignotus* is immediately distinguishable from typical epigean species by the reduced eyes, depigmented cuticle, and other modifications for subterranean life (Fig. 37.86). From *Sinodytes* and *Comaldessus* the genus differs in the presence of distinctive metacoxal lines.

Fig. 37.86. *Trogloguignotus concii.* Scale = 1.0mm.

Given the variability within the Australian subterranean *Limbodessus*, the Venezuelan *Trogloguignotus* is difficult to diagnose from those species. *Trogloguignotus* also has (1) the basal pronotal striae present (Fig. 37.86), (2) the anterior margin of the clypeus unmodified (Fig. 37.86), (3) the basal elytral stria present (Fig. 37.86), and (5) the epipleuron without a transverse carina at the humeral angle.

Classification. *Trogloguignotus* affinities with other genera is uncertain. It is mentioned by, for example, Spangler and Barr (1995), Watts and Humphreys (2006; 2009), and Michat *et al.* (2012).

Diversity. *Trogloguignotus* includes the single species *T. concii* Sanfilippo.

Natural History. *Trogloguignotus concii* is known from a cave in the karst region of La Sierra de San Luis, Venezuela. Other than its subterranean habits, nothing is known of its natural history.

Distribution. The single species is found in Cueva de Rio Gueque, Estado Falcon, Venezuela (Map 37.42).

Map 37.42. Distribution of *Trogloguignotus*.

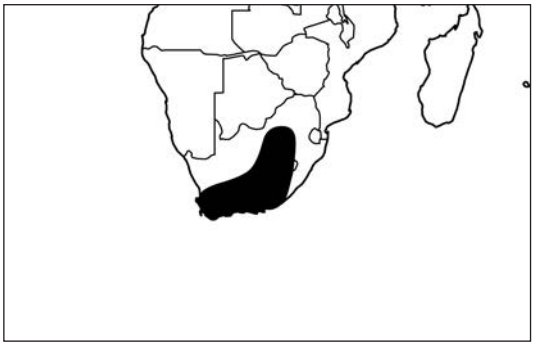
Fig. 37.87. *Tyndallhydrus caraboides.* Scale = 1.0mm.

Genus *Tyndallhydrus* Sharp, 1882

Body Length. 3.0–3.2mm.

Diagnosis. *Tyndallhydrus* are characterized by the following character combination (Fig. 37.87): (1) the head with a transverse occipital line; (2) the anterior clypeal margin is unmodified; (3) the pronotum has a pair of basal striae; (4) the elytron does not have basal or sutural striae or longitudinal carinae; (5) the epipleuron does not have a transverse carina at the humeral angle; and (6) the prosternal process does not reach the metaventrite and the mesocoxae are contiguous posterior to the prosternal process (Fig. 37.40a). The single species in this group, *T. caraboides* Sharp, is unique in Bidessini because of the shortened prosternal process, a feature characteristic of other Hydroporinae, particularly those that are rheophilic (e.g., Larson, 1991a).

Classification. *Tyndallhydrus* was described to include the one species currently in the genus by Sharp (1882). Other species have been placed in the genus but were later moved to *Sharphydrus* Omer-Cooper.



Map 37.43. Distribution of *Tyndallhydrus*.

Diversity. There is a single species in this genus, *Tyndallhydrus caraboides*.

Natural History. *Tyndallhydrus caraboides* is found in small reservoirs and streams (Omer-Cooper, 1958c).

Distribution. This genus is endemic to South Africa (Map 37.43).

Genus *Uvarus* Guignot, 1939

Body Length. 1.1–2.8mm.

Diagnosis. *Uvarus* are characterized by the following character combination (Fig. 37.88): (1) the head does not have a transverse occipital line; (2) the anterior clypeal margin is unmodified; (3) the pronotum has a pair of basal striae; (4) the elytron has a basal stria, or rarely lacking; (5) the elytron does or does not have a sutural stria; (6) the epipleuron does not have a transverse carina at the humeral angle; (7) the body form is at least somewhat elongate with the lateral outline approximately continuous or not strongly discontinuous between the pronotum and elytron, though some are more robust (Fig. 37.6b); and (8) the lateral lobe of the male aedeagus is two-segmented with the apex terminating in a small, curved, tooth-shaped lobe (Fig. 37.23b). This genus is highly generalized and includes species from throughout the world that may or may not be closely related.

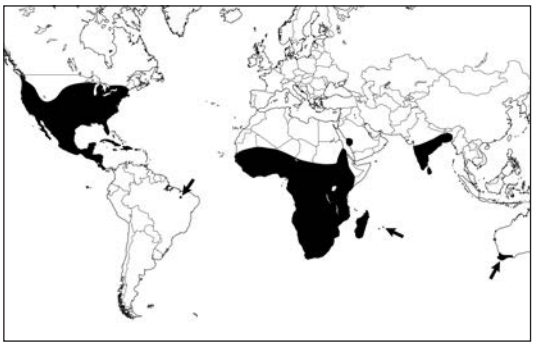
Classification. There are a large number of species in this genus, but because it appears to be characterized by plesiomorphies, many of these species may not actually be closely related. This genus has been the repository for generalized Bidessini that lack a transverse occipital line on the head but do not have other distinctive features. There are some poorly placed species in South America, Southeast Asia, and Australia that need additional investigation. The group is in considerable need of a broad phylogenetic revision.

Fig. 37.88. *Uvarus texanus*. Scale = 1.0mm.

Diversity. This is a large genus with currently 65 species. Regional revisions have included the African species by Biström (1988d; 1995) and the Indian species by Vazirani (1968). Most North American species can be identified using Larson *et al.* (2000), though several from the southwestern United States south through Mexico into Central America have not been adequately treated, and there may be new species or synonymies in this region. There may be new species in northern South America, as well.

Natural History. These species are found in many different habitats where they can often be extremely abundant. They often come to lights. At least one species currently assigned to *Uvarus*, *U. chappuisi* (Peschet) is subterranean in Burkina Faso, though Biström (1988d) was uncertain about its assignment to the genus. *Uvarus* larvae have been described by Matta (1983).

Distribution. Species currently assigned to *Uvarus* are found in North, Central, and South America; the Caribbean islands; much of Africa; India; Malaysia; and southwest Australia (Map 37.44).



Map 37.44. Distribution of *Uvarus*.

Genus *Yola* Gozis, 1886

Body Length. 1.5–3.0mm.

Diagnosis. *Yola* are characterized among Bidessini by the following (Figs. 37.24d,89): (1) the transverse occipital line is present; (2) the anterior clypeal margin is unmodified; (3) the basal elytral stria is pres-

Fig. 37.89. *Yola tuberculata.* Scale = 1.0mm.

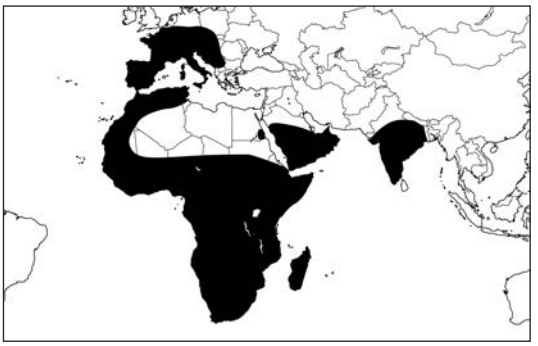
ent; (4) a pair of basal pronotal striae are present; (5) the elytral sutural stria is absent; (6) the lateral lobe of the male aedeagus is two-segmented; (7) there is no transverse carina across the epipleuron at the humeral angle; (8) the elytron has a prominent longitudinal carina on the disc; (9) the basal pronotal striae are not connected by a transverse furrow, which distinguishes this taxon from *Anodocheilus*; and (10) there is no linear series of punctures on the elytron, which distinguishes this taxon from *Yolina* and *Anodocheilus* (Fig. 37.24e). The genus is extremely similar to *Sharphydrus*. These beetles are often robust, and many have distinct color patterns (Fig. 37.89).

Classification. *Yola* used to include the subgenus *Yolina* until that group was elevated to genus rank by Biström (1983d). Apart from with *Yolina*, the genus is likely closely related to *Tyndallhydrus* and *Sharphydrus* (Ribera *et al.*, 2008).

Diversity. This large genus currently has 47 species. Most were revised by Biström (1983d) with subsequent papers describing additional new species (Biström, 1987d; 1991a; Hendrich, 1994). Many undescribed species are also known from Madagascar including one with reduced eyes with a likely interstitial or hyporheic lifestyle (Bergsten, unpublished).

Natural History. Specimens have been collected from lights but also from many other habitats from pools and streams to marshes (Biström, 1983d).

Distribution. *Yola* are found in southern and central Europe, and throughout Africa, including Madagascar, India, and the southern Arabian peninsula (Map 37.45).



Map 37.45. Distribution of *Yola*.

Genus *Yolina* Guignot, 1936

Body Length. 2.1–2.8mm.

Diagnosis. *Yolina* are characterized among Bidessini by the following (Fig. 37.90): (1) a transverse occipital line present; (2) the anterior clypeal margin unmodified; (3) the basal elytral stria present; (4) a pair of basal pronotal striae present; (5) an elytral sutural stria absent; (6) the male lateral lobe of the aedeagus two-segmented; (7) without a transverse carina across the epipleuron at the humeral angle; (8) the elytron with prominent longitudinal carinae on the disc; (9) the basal pronotal striae not connected by a transverse furrow (Fig. 37.24c), which especially distinguishes this taxon from *Anodocheilus* (Fig. 37.24e); and (10) a linear series of punctures on the elytron, which especially distinguishes this taxon from *Yola* (Fig. 37.24e). These beetles are often robust, and many have distinct dorsal color patterns (Fig. 37.90).

Classification. The genus used to be treated as a subgenus of *Yola* (see above). More recently, Wang (2015) transferred the subgenus *Yoloides* from

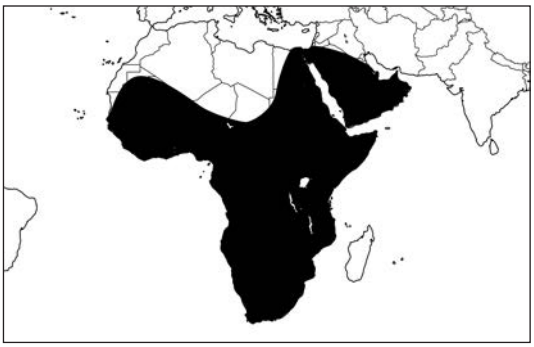
Fig. 37.90. *Yolina wewalkai.* Scale = 1.0mm.

Pachynectes to *Yolina,* which we have not followed here (see discussion under *Pachynectes*). It is very likely, however, that the two genera are closely related (Wang, 2015).

Diversity. *Yolina* currently includes 12 species, and the genus was revised by Biström (1983d), who added new species and clarified others in later papers as well (Biström, 1987a; e; 1991b).

Natural History. *Yolina* have been collected from many habitat types, including streams and ponds, though many specimens in collections are from lights (Biström, 1983d).

Distribution. This group is characteristic of central Africa but extends through the southern Arabian peninsula (Map 37.46).



Map 37.46. Distribution of *Yolina*.

Genus *Zimpherus* Miller and Wheeler, 2015

Body Length. 2.0–2.2mm.

Diagnosis. The single species of *Zimpherus* has the following diagnostic combination (Fig. 37.91): (1) a transverse occipital line on the head absent; (2) the anterior clypeal margin unmodified; (3) a transverse carina across the elytral epipleuron at the humeral angle absent; (4) the basal elytral stria present; (5) the elytral sutural stria absent; (6) the elytron without rows of punctures; (7) the lateral lobes of the male aedeagus with two segments and apically broadly rounded (Fig. 37.21); and (8) the median lobe of the male aedeagus apically complex and multifid (Fig. 37.21). The dorsal body shape is narrowed anteriorly, and the head is somewhat deflexed ventrad (Fig. 37.91). The genus differs from *Uvarus*

Fig. 37.91. *Zimpherus nancae.* Scale = 1.0mm.

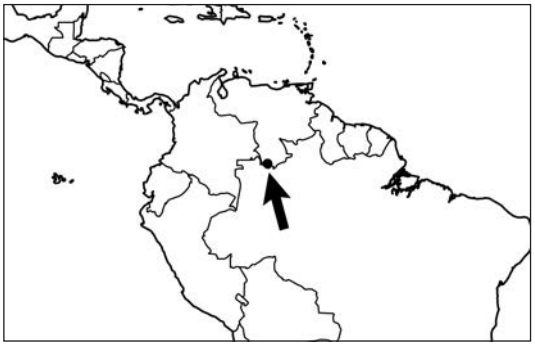
in the unusual body shape, the median lobe is apically multifurcated and multilobed, and the lateral lobe is broad with the apex rounded (Fig. 37.21), without the small, curved, tooth-shaped lobe characteristic of *Uvarus* (e.g., Fig. 37.23b). The genus differs from members of *Microdessus* in larger size, dramatically offset metatrochanter (Fig. 37.20a), and overall shape, though both share unusual modifications to the male median lobe (Figs. 37.21,22).

Classification. Relationships of this genus to others in Bidessini are not yet known.

Diversity. There is a single species in this genus, *Z. nancae* Miller and Wheeler.

Natural History. Series of this species were collected at a black light in rainforest habitat (Miller and Wheeler, 2015).

Distribution. This genus is known only from near Cerro de Neblina, Venezuela (Map 37.47).



Map 37.47. Distribution of *Zimpherus*.

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